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Small-Scale Plant Species Composition and Diversity in Relation to Environmental and Disturbance Factors in Fescue Grasslands of the Aspen Parkland of Alberta

BY

KSENIJA VUJNOVIC ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE

DEPARTMENT OF BIOLOGICAL SCIENCES

EDMONTON, ALBERTA
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UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled SMALL-SCALE PLANT SPECIES COMPOSITION AND DIVERSITY IN RELATION TO ENVIRONMENTAL AND DISTURBANCE FACTORS IN FESCUE GRASSLANDS OF THE ASPEN PARKLAND OF ALBERTA, submitted by KSENIJA VUJNOVIC in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE

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ABSTRACT

A comprehensive study was conducted in the summer of 1996 in remnant grasslands across the aspen parkland in order to associate plant species composition with environmental conditions and small-scale disturbances, and to relate plant species diversity to the levels of disturbance. A total of 490 $1m^2$ quadrats were established in 11 grassland remnants. For each quadrat, percentage cover of plant species, litter height, percentage cover of exposed mineral soil, slope and aspect were recorded, and a soil core was collected for soil analyses. Each quadrat was assigned to one of ten levels of disturbance. Direct gradient analyses related species composition to environmental and disturbance variables. Different diversity indices were calculated and related to the disturbance levels; polynomial regressions were used to test the Intermediate Disturbance Hypothesis. Direct gradient analyses indicated that disturbance is a major factor influencing small-scale plant species composition in remnant grasslands. *Festuca hallii* dominates undisturbed areas, while species composition in disturbed areas depends on the magnitude of the disturbance and environmental conditions, such as moisture, sodicity, and nitrogen levels. It was demonstrated that the majority of exotic species prefer disturbed and moist areas. The Intermediate Disturbance Hypothesis was supported regardless of the measure of diversity used. Richness of exotic (not native to North American continent) vascular plant species showed a significant but weak positive relationship with the magnitude of the disturbance; native species richness predominated over exotic species richness at all levels of disturbance. It is also suggested that the assembly of plant species in fescue grasslands may follow the "centrifugal organization model" previously discussed only for forest and wetland communities. *Festuca hallii* dominates the relatively undisturbed ("core") habitat, while the composition of plants in the "peripheral" habitats depends on the magnitude of the disturbance and environmental conditions. Finally, recommendations regarding management of remnant grasslands are given.

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CHAPTER 1
GENERAL INTRODUCTION

Background Information

The Aspen Parkland Ecoregion of Alberta (Strong and Leggat 1992), also called Central Parkland Sub-region (Achuff 1994), is the third largest ecoregion in Alberta, covering approximately 7.9% of the province (Strong and Legat 1992). It represents the largest remaining block of parkland in the world (Anonymous 1997). Moss (1932) defined parkland, or the "grove belt", as "a transition or tension belt which lies between the poplar area and the prairie. This belt consists of aspen groves and patches of prairie grassland, more or less uniformly intermixed". In their overview of the aspen parkland, Bird (1961) and North (1976) indicated the change in the area covered by grasslands and aspen groves along the latitudinal gradient and related it to the past and present climate in the area. On the northern fringe of the parkland, tree groves cover the majority of the area compared to the intermingling grasslands. At lower latitudes and at the southern fringe of the parkland, aspen stands become small islands within an extensive grassland cover. Plains rough fescue, *Festuca hallii* (Vasey) Piper, is an important indicator of native grasslands of the aspen parkland.

At present, less than 5% of the aspen parkland remains in the pre-settlement conditions (Van Tighem 1993). In addition to being the most densely populated ecoregion of Alberta, it is well suited to crop and grazing systems that have either completely destroyed or altered native plant communities to various degrees (Bird 1961). Fescue grasslands, including these of the parkland, are one of the most threatened biogeographical regions in Canadian Prairie Provinces. They cover about 5% (Weins 1996) or even less (Diamond 1993) of their original area. Fire suppression and the extinction of the plains bison (*Bison bison bison* L.) in the region significantly altered the proportion of grasslands that was present at the beginning of the century (Bailey and Wroe 1974, Campbell et al. 1994). Urbanization, intentional introduction of exotic species into pastures, domestic stock overgrazing, and tree and shrub invasion represent

constant threats to the natural balance between tree and grass communities, and especially to the populations of native plants in remnant grasslands (Anonymous 1997).

Native plant populations of remnant grasslands in the aspen parkland contribute to species and habitat diversity. Recent attempts by Elk Island National Park and a number of private landowners to reintroduce native prairie on disturbed lands within the aspen parkland (Dana Bush, personal communications) show the importance of better understanding the ecology of existing plant populations in remnant grasslands. Most likely, native species from remnant grasslands are genetically different from conspecific populations outside the aspen parkland zone, in response to the specific microclimate conditions and vegetation composition (for discussion see Handel et al. 1994). Therefore, they could play an important role in land revegetation and ecological restoration of disturbed areas within the aspen parkland. Handel et al. (1994) summarized the results of many North American studies, confirming the importance of already adapted genotypes for the success of restorations and recognized "genetic pollution" as a threat to conservation of natural populations. They highlighted the importance of the knowledge about species composition of highly diverse native communities adapted to different disturbance regimes and variety of environmental conditions, such as topography and soils.

Studies on plant species diversity and stability in grassland communities have also shown that diverse, native plant communities can resist major environmental perturbation, such as drought, floods, and insect invasions. Loss of native plant diversity may strongly influence ecosystem productivity, sustainability, and stability (review by Elton 1958, and Denslow 1985, and experimental studies by Naeem *et al.* 1994, Tilman and Downing 1994, Tilman 1996, and Tilman et al. 1996). Species-rich communities are also believed to be less susceptible to invasion by exotic species (Fox and Fox 1986). Handel et al. (1994) emphasized the importance of native plant species diversity for diversity of insects. Murdoch et al. (1972) found high positive correlation between diversity of plants and that of associated plant-sucking bugs (Homoptera) in Michigan, USA. The complex evolutionary relationships between butterflies and their food plants, that have been

discussed by Ehrlich and Raven (1964), suggest the importance of the native species diversity for the existence of co-evolved species of butterflies.

Aside from being important at the local scale (within the remnant), the diversity of native plant species can be very important on a larger (landscape) scale. The importance of the extension of natural pastures in good native condition for the maintenance of viable native plant populations across the landscape has already been recognized for Australian grasslands (McIntyre and Lavorel 1994a). However, a small grassland remnants may also play an important role during the large scale events such as global climatic warming. Schwarz et al. (1997) reviewed ecological modeling studies that showed a relationship between global warming and grassland expansion and hypothesized that within the Low Boreal and Mid Boreal Mixedwood Ecoregions of Alberta (two ecoregions adjacent to the Aspen Parkland Ecoregion), isolated dry grasslands will become essential genetic reservoirs from which expansion of native plant populations can take place. They also reported much higher numbers of vascular grassland species for the Aspen Parkland (122) then for the Low Boreal (68) or Mid Boreal Mixedwood (41) Ecoregions. Under global warming, diverse native grasslands within the aspen parkland may serve as genetic nuclei for grassland expansion, as well as corridors for movement of southern prairie species toward grasslands located in northern ecoregions.

Although limited information is available for native grasslands within the aspen parkland of Alberta (Moss and Cambell 1947, Wroe 1971, Wheeler 1976), there are strong indications that local plant species composition and diversity depend on different environmental conditions and overlying effects of disturbance. Moss and Campbell (1947) noted that the late successional species, *Festuca hallii,* dominated undisturbed areas to the exclusion of other species. However, when intensively grazed, native grasslands become dominated by more grazing-tolerant species, such as *Agropyron trachycaulum* var. *trachycaulum* (Link) Malte, *Poa pratensis* L., *Danthonia californica* Boland, *Bouteloua gracilis* (HBK) Lag., and *Artemisia frigida* Wiolld. (Moss and Campbell 1947). The authors warned that the final outcome of the plant community composition depends on other local conditions, such as soil type. In addition, there is

agreement among scientists that the diversity of plant species can be associated with the level of habitat disturbance (see Collins and Glenn 1988, Martinsen *et al.* 1990, McIntyre and Lavorel 1994a, b). Therefore, grazing at different intensities and small-scale soil disturbances, such as animal burrows, bison wallows, and cow paths, can play an important role in the natural selection and diversity of plant species at the small scale in remnant grasslands.

Another important aspect of the disturbance in plant communities is invasion by exotic species. A significant portion of the North American flora now consists of exotic species (Forcella and Harvey 1983b, Mooney and Drake 1986, Randall and Marinelli 1996), invading agricultural and other disturbed areas of the New World since the earliest days of European settlement. Elton (1958) reviewed some population explosions of exotic plant species throughout the world that have resulted from highly suitable habitats and lack of natural predators. Groves and Burdon (1986), Mooney and Drake (1986), and Drake et al. (1989) summarized many dimensions of exotic plant species invasion on the North American and Australian continents. Although a number of exotic plant species, such as *Lythrum salicaria* L., *Clematis vitalba* L., and *Bromus inermis* ssp *inermis* Leyss., have shown an ability to modify the composition of native vegetation (White et al. 1993, Cronk and Fuller 1995, and Randall and Marinelli 1996), there is considerable evidence that exotic species invasion requires some level of anthropogenic disturbance (Groves and Burdon 1986, Mooney and Drake 1986, D'Antonio and Vitousek 1992).

Along with the loss of grassland habitat by land fragmentation, native plant populations in the aspen parkland may be threatened by exotic species invasion. Christiansen (1990) and Tyser and Christopher (1991) found that exotic species have the ability to replace native grassland vegetation by expansion from disturbed road rights-of-way, where exotics initially become established. Forcella and Harvey (1983a, b) also suggested that roadsides may attribute to the exotic species proliferation. Motor vehicles are held partially responsible for the dispersal of seeds and other propagules along roadsides into already disturbed vegetation of road rights-of way (Schmidt 1989), and roads in the Aspen Parkland Ecoregion have a density of 0.85 km/km^2 (Anonymous 1997). The extent

of exotic species invasion on remnant grasslands has not been studied in the parkland ecosystem. Significant data on exotic species invasion within the aspen parkland have been collected only from conservation areas (Blyth and Hudson 1987, Achuff 1990, Bork 1993). According to Achuff (1990), Elk Island National Park contains at least 57 exotic species, or ca. 14% of the park's flora (426 species in total). Studies from areas other than the aspen parkland indicated a positive relationship between the abundance of exotic plant species and the level of disturbance (Fox and Fox 1986, McIntyre and Lavorel 1994a, b, Kotanen 1995). Moreover, the expansion of crop fields in the aspen parkland and the alteration of native plant communities by cattle grazing have caused changes in the composition of animal species, which further influenced changes in the native flora (Bird 1930, 1961, North 1976). Moss and Campbell (1947), Wroe (1971), and Wheeler (1976) studied a small number of rather scattered remnant grassland communities within the aspen parkland but provided limited information on exotic species.

Determining the small-scale plant species composition in the remnant grasslands of the aspen parkland and relating composition to the underlying environmental conditions, including those related to the small-scale disturbances can provide better understanding of the ecology of present native grasslands and the possible threats by exotic species. In addition, understanding how habitat disturbance influences plant species diversity with respect to richness and abundance can provide useful information on both native and exotic species. The results of this study may assist in the decision-making process regarding the management of land for different purposes (conservation, native seed collection, wildlife management, or cattle grazing).

Objectives

The objectives of this study were to investigate a number of remnant prairie grasslands within the aspen parkland (1) to determine small-scale (1 m^2) vascular plant species composition and to relate that composition to the environmental conditions and overlying disturbances; (2) to determine the relative importance of environmental conditions and overlaying disturbances for exotic vascular plant species invasion; (3) to suggest what model best describes the assembly of vascular plant species in fescue grasslands along

disturbance and environmental gradients; (4) to assess the importance of small-scale (1 m^2) disturbances on native and exotic plant species diversity; and (5) to suggest actions for managing prairie remnants in the aspen parkland.

Description of the study area

The term "aspen parkland" is used in this study only for the larger, northern portion of the Aspen Parkland Ecoregion of Strong and Legat (1992), which, to a great extent, overlaps with the Central Parkland Sub-region of the Aspen Parkland Natural Region (Achuff 1994). Figure 1-1 indicates the position of the Aspen Parkland Ecoregion in Alberta. The aspen parkland, as defined in this study, lies between 51° 10' and 54° 00' latitude and 110° 00' and 114° 10' longitude. The portion of the Aspen Parkland Ecoregion (Strong and Legat 1992) south of the Cremona-Airdrie line (Figure 1-2), defined as the Foothills Sub-region of the Aspen Parkland Natural Region by Achuff (1994), was not included in this study. Foothills Sub-region has been examined more intensively than the Central Parkland Sub-region and the differences in grassland composition between these two areas has been reported in a number of papers (Moss 1944, Moss and Campbell 1947). Moss and Campbell (1947) differentiated the southern from the northern portion of the area by the southern being richer by at least 50 vascular plant species and by the significant increase in *Festuca idahoensis* Elmer and *Danthonia parryi* Scribn. The richer flora of the southern parkland was related to the proximity of other vegetation types, especially from the mountains, and to the greater time elapsed since the last glaciation that affected the region. In addition, in the foothills area *Festuca campestris* Rydb. (Looman 1982) is the predominant rough fescue species.

Topography and soils

The region has an undulating to hilly topography resulting from the last glaciation ca. 10,000 years ago. Various types of glacio-fluvial, morainic, and lacustrine deposits, with glacial till being the most common, form the surface deposits. A relatively shallow mantle of till deposited by melt water from glaciers resulted in a rolling terrain, while undulating and gently rolling surfaces indicate a deep till mantle where the glacier melted *in situ* (Coupland and Brayshaw 1953). Dark Brown Chernozems with sandy loam

texture and Black Chernozems with loam and clay-loam texture developed under grasslands and upland shrub communities, whereas "deep" Dark Gray Chernozems developed under prolonged aspen occupation (Moss and Campbell 1947). The authors related the development of the bulk of organic matter in the black soils to a single species, *Festuca hallii*, and indicated that on Dark Brown Chernozems, the *Festuca hallii* association intermixes with elements of the brown soil zone, *Stipa* spp., *Agropyron smithii* Rydb., and *Bouteloua gracillis*. Black and Dark Brown Chernozems occur in regions of cooler and moister environments, where the A horizon has 0.40 to 0.70 and 0.15 to 0.35 % nitrogen, respectively (Mitchell and Moss 1948). In addition, some grassland communities within the aspen parkland developed on coarse sandy soils (Regosols) and on Black Solonetzic or Dark Brown Solonetzic soils (Coupland 1961). Solonetzic soils appear where saline bedrock shales are exposed or comprise the bulk of the drift. These soils are influenced by the lack of lime and by the fine texture of the parent material (Coupland 1961). Moderately to imperfectly drained Black Chernozemic soils support willow communities (Moss 1932). In general, most soils occupied by grassland vegetation developed on morainal, fluvioglacial, or aeolian parent material, but some are on alluvial or lacustrine parent material. They are weakly to strongly calcareous and well to moderately well drained (CANSIS - NSDB).

Climate

Strong and Leggat (1992) suggested that climatic conditions within the Aspen Parkland Ecoregion are distinctly different from the two adjacent ecoregions, the Mixed Grass and the Low Boreal Mixedwood Ecoregions. The mid-Alberta storm track has its influence on the climate in the region. Summer precipitation reaches its peak earlier in the summer in the Mixed Grass Ecoregion, whereas July is the month with the highest precipitation in the Aspen Parkland Ecoregion. In comparison with the Mixed Grass Ecoregion, the Aspen Parkland Ecoregion has a greater number of days with measurable precipitation, the duration of snow cover tends to be longer due to colder temperatures and less wind ablation, and the summer potential evapotranspiration is significantly lower. Although there is no substantial difference in the mean summer temperature between these ecoregions, the mean annual temperature in the Aspen Parkland Ecoregion is lower than

in the Mixed Grass Ecoregion but higher than in the Low Boreal Mixedwood Ecoregion. The Aspen Parkland Ecoregion is also wetter compared to the Low Boreal Mixedwood Ecoregion. A summary of the general climatic conditions for the Aspen Parkland, Mixed Grass, and Low Boreal Mixedwood Ecoregions is presented in Table 1-1.

Some of the important climatic conditions characterizing the Aspen Parkland Ecoregion have been neglected. As reported by Wyatt et al. (1944) and Pettapiece (1995), there is a spatial moisture gradient within the aspen parkland, with the available moisture increasing from the southeast to the northwest (Figure 1-2). The moisture index has been determined by subtracting potential evapotranspiration from the precipitation for the period from May to August (Pettapiece 1995). Although developed for agricultural purposes, this moisture gradient may be viewed as a gradient of favorable growth conditions on a landscape scale for native vegetation as well (Pettapiece, personal communications). A different set of climatic moisture index values (annual climatic moisture index) also supports the existence of a southeast-northwest moisture gradient (Figure 1-2) (for more details see Campbell et al. 1994 and Hogg 1994).

Vegetation description - literature review

As a transitional zone between the prairie grassland to the south and the boreal forests to the north, the vegetation of the Aspen Parkland Ecoregion consists of aspen stands and shrub communities in moist habitats intermingled with grasslands on drier, south or southeast-facing sites (Strong and Leggat 1992). General descriptions of the grassland vegetation within the Aspen Parkland Ecoregion of Alberta (Moss 1932, Bird 1961, North 1976) provide some information that pertains to the present day grassland remnants. Dominant shrub species described by these authors were *Symphoricarpos* spp. Duhamel, *Rosa* spp. L., *Elaeagnus* spp. L., and *Shepherdia canadensis* (L.) Nutt. Dominant grass species were the northern prairie grass species *Festuca hallii*, *Agropyron* spp. Gaertn., *Helictotrichon hookeri* (Scribn.) Henr., *Poa interior* Rydb., and the southern prairie species *Koeleria macrantha* (Ledeb.) J.A. Schultes f., *Stipa comata* Trin. & Rupr., and *Bouteloua gracilis*. Moss and Campbell (1947) provided a detailed description of grasslands around Edmonton, Vermilion, Alix, Drumheller, and Hand Hills. Based on the

visual estimation of the area, they recognized one main grassland association as "virgin" grasslands, a *Festuca scabrella* (Torr.) association, and emphasized that *F. scabrella* dominated the undisturbed grasslands to the exclusion of most other associated species. They also indicated that the species of the light brown soil zones, *Stipa comata, Agropyron smithii,* and *Bouteloua gracillis*, inhabited very dry, south-facing slopes within the aspen parkland. However, they suggested that the overall composition of the fescue grassland depended on soil conditions and herbivory. On many overgrazed areas, the composition of grasslands has changed by the expansion of more grazing-tolerant grass and grass-like species, such as *Agropyron trachycaulum* var. *trachycaulum*, *Stipa curtiseta* (A. S. Hitchc), *Poa pratensis*, *Danthonia californica*, *Bouteloua gracilis,* and *Carex pensylvanica* Lam., and forbs, such as *Artemisia frigida* and *Gutierrezia sarothrae* (Pursh) Britt. & Rusby. No quantitative data were provided to support their observations.

Coupland (1950, 1961) recognized the *Festuca scabrella* association as a unique association in grasslands of the Northern Great Plains of North America. However, it was not until 1982 that three dominant *Festuca* species have been recognized within the *Festuca scabrella* association: *Festuca hallii*, *F. campestris*, and *F. altaica* (Trin.) (see Pavlik and Looman 1984 for differences in species morphology, ecology, and geographical distribution).

Aside from the undisturbed "virgin" fescue community, numerous other communities have been described in the aspen parkland to date. Looman (1980) described communities on sandhills within the aspen parkland as dominated by *Calamovilfa longifolia* (Hook.) Scribn. Wheeler (1976) described five main plant communities in the area near Kinsella by using clustering and ordination techniques: *Symphoricarpos occidentalis*, *Symphoricarpos-Festuca*, *Festuca-Stipa*, *Stipa-Festuca*, and *Stipa-Agropyron*. Wroe (1971) gave a detailed description of the grassland vegetation within one quarter section of the Rumsey Ecological Reserve, where he recognized five grassland communities: *Symphoricarpos occidentalis, Festuca scabrella*, *Festuca-Stipa*, *Stipa-Artemisia*, and *Koeleria-Agropyron*. This study suggested that in the southern portion of the aspen parkland, *Festuca hallii* tends to occupy somewhat moister

microclimates, with a mean canopy cover of 84%. Quantitative statistics supported the conclusions of the last two authors.

Valuable information on grassland composition within the aspen parkland of western Canada originated from studies in Saskatchewan (Coupland and Brayshaw 1953). Coupland and Brayshaw (1953), who described grasslands based on quantitative data, reported the dominance of *Festuca hallii* grasslands in the northern portion and the codominance of *Stipa curtiseta* within the southern fringe of the aspen parkland. Although it was difficult to compare their quantitative data with visual estimate by Moss and Campbell (1947), Coupland and Brayshaw (1953) recognized that the dominant grass species (*Festuca hallii*) did not cover the ground to the extent suggested by Moss and Campbell (1947). Coupland and Brayshaw (1953) related this discrepancy to the lack of precision of the non-quantitative visual estimation and to the possible more intense past grazing on the Saskatchewan study sites. Looman (1982) recognized the *Festuca hallii* alliance for these aspen parkland grasslands. *Festuca hallii*-dominated grasslands were also found within Prince Albert National Park in Saskatchewan (Carbyn 1971), and in the western portion of Riding Mountain National Park, Manitoba (Blood 1966).

Methods

Selection of remnants

Only those areas that had never been cultivated and were unmodified by overgrazing or soil removal on a larger scale were selected for this study. Well-drained, level to undulating areas and moderate slopes were preferred, but moderately drained soils on Solonetzic soils were included. Aerial photographs were used to help locate areas of unbroken land (Vujnovic and Wein 1997). Eleven remnant areas separated spatially by cultivated land were chosen for the study. Based on geographical position and local soil characteristics, they were divided into four regions: Elk Island National Park, Kinsella, Wainwright, and Rumsey (Figure 1-3). Remnants include a variety of soils (Black Chernozem, Dark Brown Chernozem, Solonetz) and topographic features (flat to hilly) (Table 1-2).

Field sampling

A total of 49 sampling blocks (each 1000 m^2) were established in 11 remnants (ca. 4 per remnant) (Figure 1-4). Blocks were chosen to include as many different types of small-scale disturbances as were available. Each disturbance represented different combinations of vegetation and soil disturbance, and disturbance is defined in this study as "a mechanism that limits the plant biomass by causing its partial or total distraction" (Grime 1979). At each block, ten 1m^2 quadrats were selected by stratified randomization (Figure 1-4). Disturbances included light grazing with no soil disturbance, moderate grazing with light soil compaction, heavy grazing with moderate soil compaction, vehicle or cow paths with heavy soil compaction, recent and old mixing of topsoil with subsoil caused by burrowing animals or small-diameter pipeline construction, and removal up to 10 cm to more than 50 cm of topsoil. Sampling of each disturbance type was conducted as follows:

Undisturbed quadrats were sampled in areas where fences prevented cattle grazing for more than 20 years.

Lightly grazed quadrats were sampled under the fence because these areas are defoliated (although not frequently) but not trampled. Similar criteria were employed by Naeth *et al.* (1990). Although Willms *et al.* (1988) suggested the existence of stable, lightly grazed patches, resulting from uneven grazing pressure, our preliminary examination (Vujnovic and Wein 1997) showed that observations during only one season were not sufficient for their identification.

Medium grazing was assumed if no disturbance other than grazing was observed, because, in general, pastures sampled have long-term controlled grazing regimes that results in the moderate grazing intensity (Barry Cole, personal communications). In areas grazed by bison and horses, medium grazing was assumed based on available historical information.

Heavy grazing was found in areas close to domestic stock water sources and in the proximity of gates (a similar method was applied by Looman 1969, 1980, and Willms et al. 1988).

Heavily trampled quadrats were sampled on farm tracks and cow paths. Weaver and Dale (1978) reported change in vegetation composition as a result of heavy soil compaction.

Mixed topsoil with subsoil occurred on burrows from animals, such as Richardson's ground squirrel (*Spermophilus richardsonii* Sabine) and badger (*Taxidea taxus* Schreber), and on pipelines. These kinds of disturbances have been investigated for changes in soil characteristics and, to a limited extent, in species composition in a number of studies (Naeth *et al.* 1987, Adams et al. 1996, Martinsen et al. 1990).

Topsoil removal at different levels was found on animal wallows, water eroded areas, scalping with machinery, and road rights-of-way.

Table 1-1. Climate conditions in the Aspen Parkland Ecoregion of Alberta, and two adjacent ecoregions, Mixed Grass and Lower Boreal Mixedwood (modified from Strong and Legat 1992).

	Lower Boreal Mixedwood Ecoregion	Aspen Parkland Ecoregion	Mixed Grass Ecoregion
Mean annual temperature	0.8 °C	3.3 °C	5.3 °C
Mean summer temperature	13.8 °C (12.5/14.7)	14.4 °C (13.5/15.2)	15.2 °C (14.0/16.0)
Maximum summer temperature	20.4 °C (19.0/21.7)	20.9 °C (19.5/22.2)	22.6 °C (21.2/24.2)
Mean winter temperature	-10.5 °C (-15.5/-7.2)	-8.7 °C (-13.5/-5.7)	-5.2 °C (-9.2/-1.7)
Minimum winter temperature	-15.8 °C (-21.0/-12.0)	-14.0 °C (-18.5/-10.7)	-11 °C (-15.5/-7.5)
Total annual precipitation	380 mm	412 mm	326 mm
Total summer precipitation	235 mm (136/356)	259 mm (157/381)	176 mm (104/272)
Total winter precipitation	61 mm (36/98)	53 mm (32/86)	52 mm (32/79)
Mean growing degree days	1150	1257	1442
Number of days <0 °C (summer)	8 (5/13)	6 (3/9)	6 (3/9)
Number of days with measurable precipitation (summer)	44 (33/55)	49 (36/61)	37 (29/47)
Number of days with measurable precipitation (winter)	28 (17/39)	26 (17/37)	20 (14/32)

Table 1-2. Legal descriptions of 11 remnant areas, grouped into the four geographical regions. Soil zones, topography and soil textures, as well as number of quadrats per remnant are presented. Information on soil zones, texture, and topography follows Wyatt *et al.* 1938, 1944, Bowser *et al.* 1973, 1976, and Crown 1977.

"Region"	Legal description for each remnant	Number of quadrats	Soil zone	Soil texture	Topography
Wainwright	NW 21-39-7 W4	40	Dark Brown	Loam	Rolling
	NW 29-41-9 W4	40	Dark Brown	Loamy Sand	Gently rolling
	NW, SW, SE 11-41-10 W4	40	Dark Brown	Loam	Rolling
Rumsey	RER (NW 23-34-19 W4)	10	Dark Brown Solodized solonetz	Loam	Rolling
	RER (NW 14-34-19 W4)	20	Dark Brown	Loam	Hilly
	RER (NW 13-34-19 W4)	10	Dark Brown	Loam	Rolling
	RER (SW 04-34-19 W4)	10	Dark Brown	Loam	Hilly
	RER (NE 31-33-19 W4)	10	Dark Brown	Loam	Hilly
	RER (NE 16-33-19 W4)	10	Dark Brown	Loam	Hilly
	RER (NE 09-33-19 W4)	10	Dark Brown	Loam	Hilly
	NW, NE, 11-38-17 W4	40	Thin Black Solodized Solonetz	Loam	Level to undulating
Kinsella	NW 28-47-11 W4	40	Shallow Black	Loam	Rolling
	NW, SW, SE 11-48-14 W4	40	Shallow Black Solodized Solonetz	Loam	Level to undulating
	NE, SE 11-46-14 W4	40	Shallow Black	Loam	Level to undulating
Elk Island National Park	EINP (NE, SE 25-53-20-W4)	20	Gray Solodized Solonetz	Loam	Undulating, depretional
	EINP (SW 07-54-19 W4)	20	Eluviated Eutric Brunisol	Loamy sand	Ridged, humocly
	EINP (NE 33-52-20 W4)	10	Eluviated Eutric Brunisol	Loamy sand	Ridged, humocly
	NE, SE 9-56-18 W4	40	Black Solodized solonetz	Loam	Undulating, depretional
	SE 17-54-18 W4	40	Black Solodized solonetz	Loam	Undulating, depretional

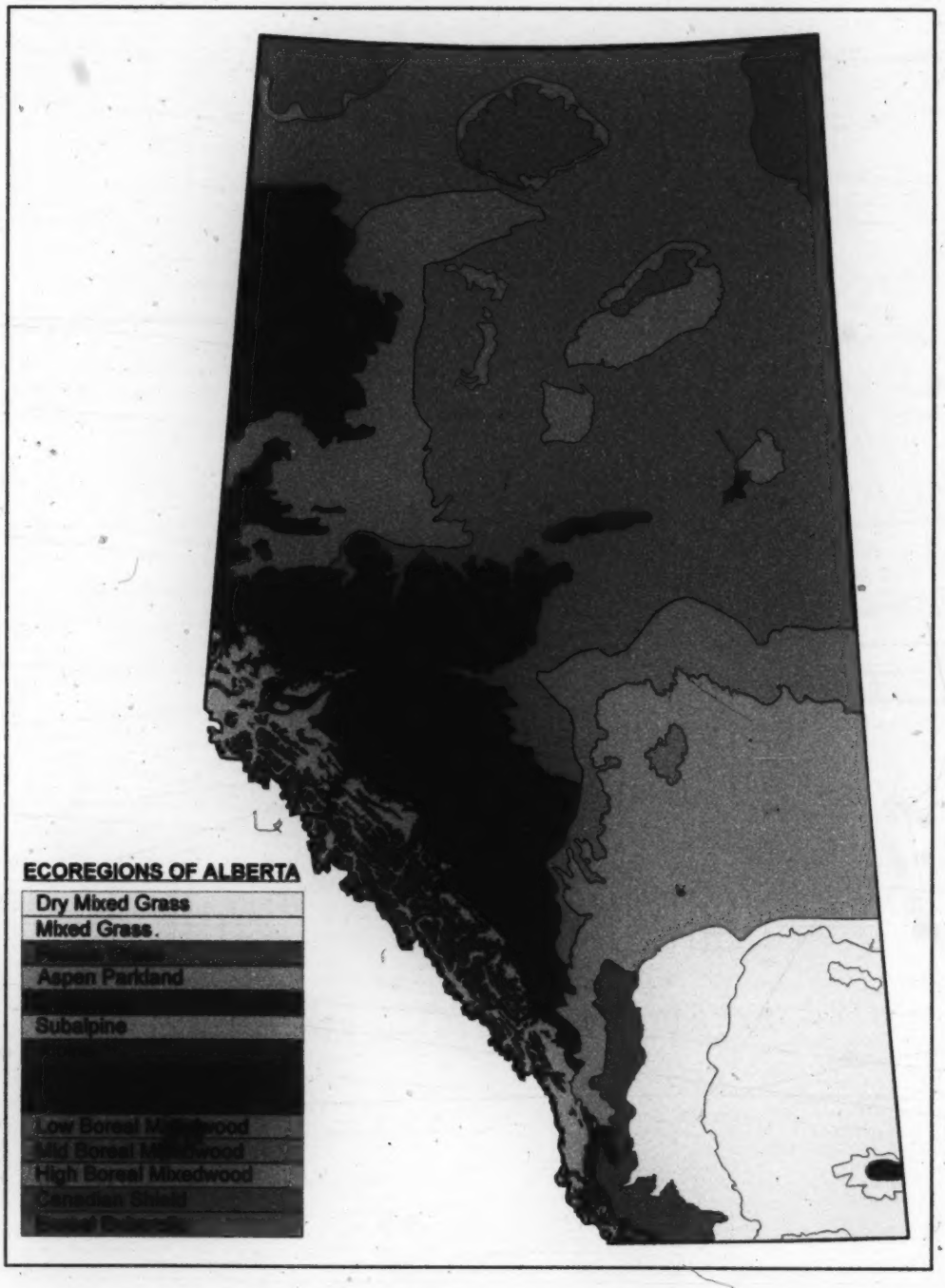

Figure 1-1. Ecoregions of Alberta (modified from Strong and Legat 1992).

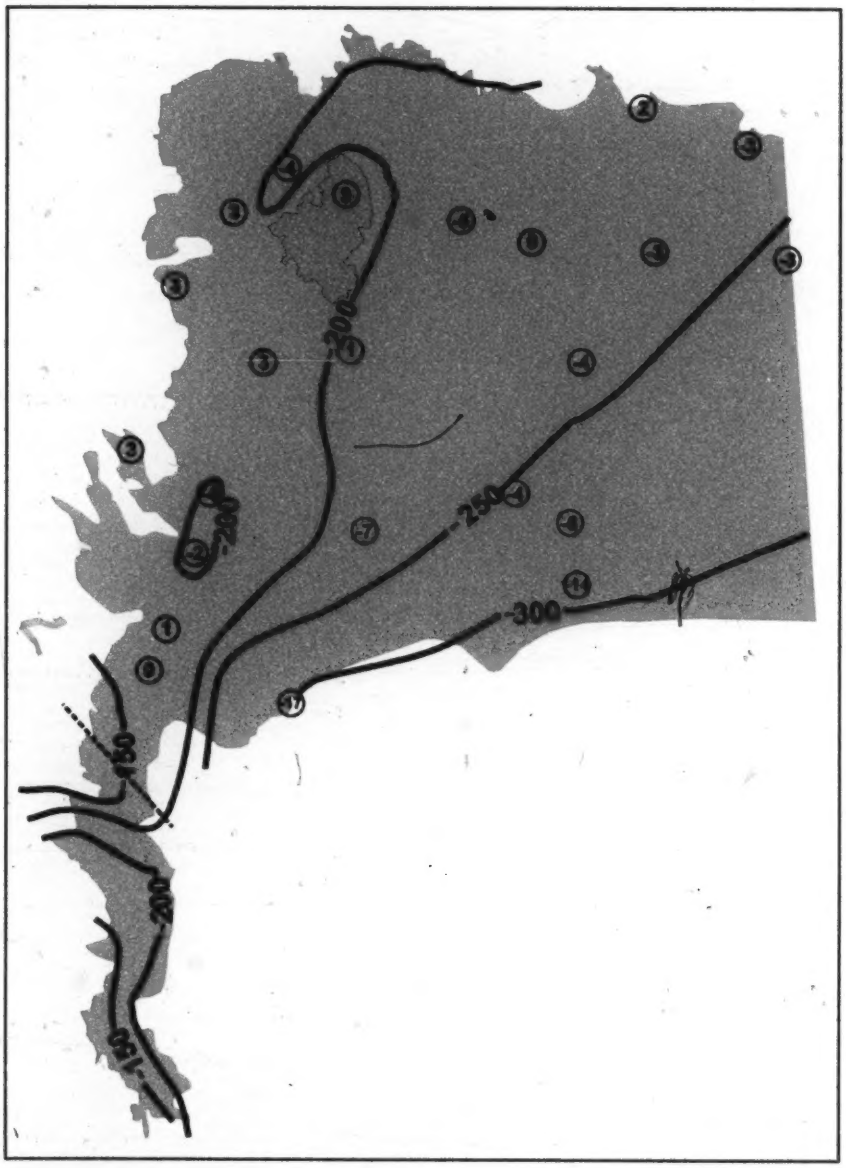

Figure 1-2. Values for the two **P-PET** climatic moisture indices (**P**recipitation minus **P**otential **E**vapo-**T**ranspiration) in the Aspen Parkland Ecoregion of Alberta; lines represent moisture index (expressed in mm) calculated for growing season (period May to August) only (modified from Pettapiece 1995); numbers in circles represent annual climatic moisture indices (expressed in cm, modified from Hogg 1995). Higher values represent moister conditions. P-PET for Elk Island National Park was provided courtesy of Dr. E. H. Hogg from the Northern Forest Services, Edmonton, Alberta. Dashed line separates the northern portion of the Aspen Parkland Ecoregion included in this study from the southern portion, defined as the Foothills Sub-region of the Aspen Parkland

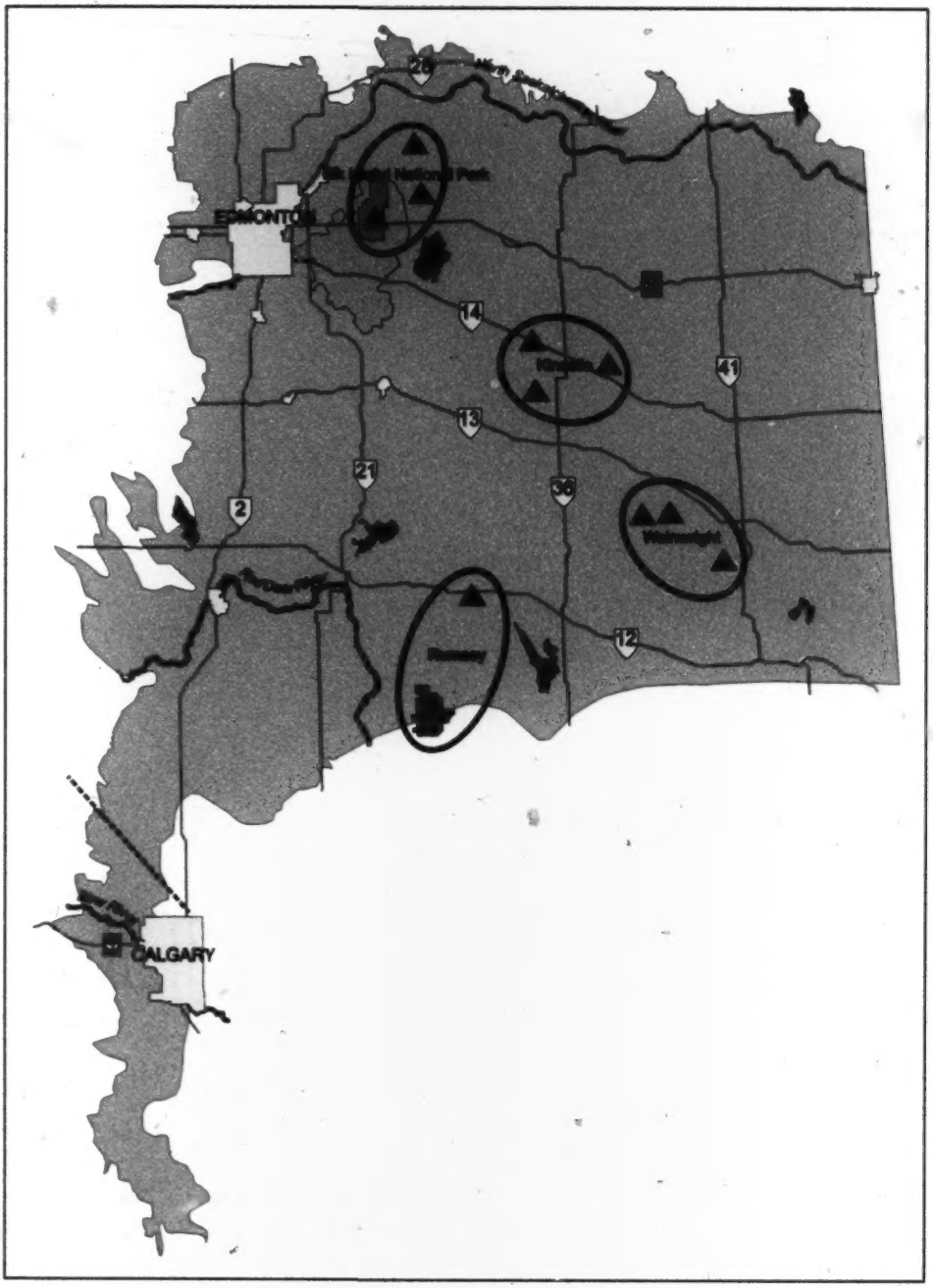

Figure 1-3. Locations of 11 areas of remnant grasslands (triangles) and four regions (circles) in the Aspen Parkland Ecoregion of Alberta (after Strong and Legat 1992); the four regions were Elk Island National Park, Kinsella, Wainwright, and Rumsey.

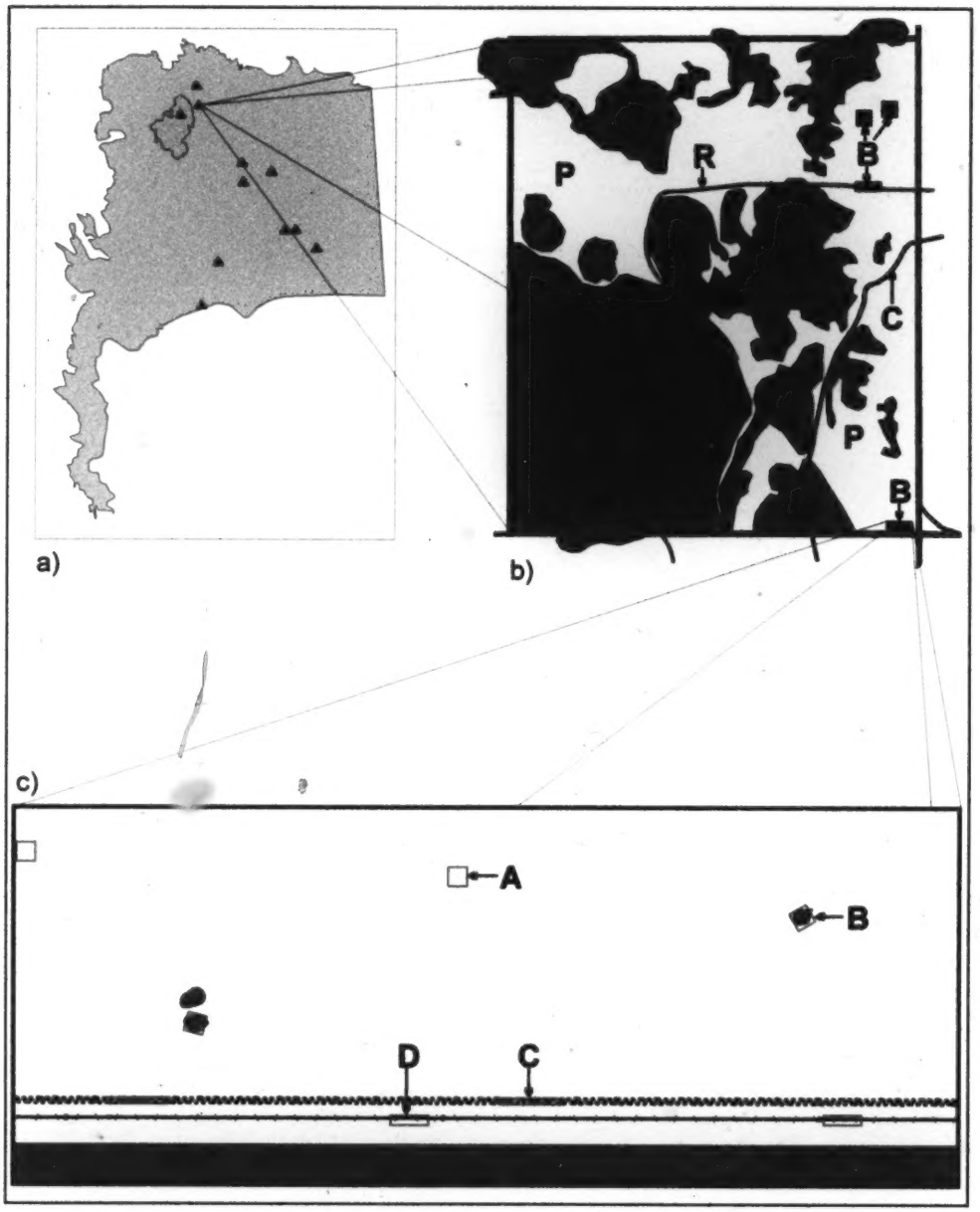

Figure 1-4. A diagram representation of a sampling design: (a) location of 11 remnant areas (triangles) in the Aspen Parkland Ecoregion; (b) an area from the Elk Island National Park region with four 1000 m^2 blocks with A - agricultural field, B - 1000 m^2 blocks, C - channel, R - road, T - trees, P - prairie, and W - wetland; (c) one block with sampling quadrats on A - medium grazing, B - animal burrow, C - cow path, D - under the fence, E - in the ditch.

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CHAPTER 2

ENVIRONMENTAL AND DISTURBANCE FACTORS DETERMINING SMALL-SCALE PLANT SPECIES COMPOSITION

Introduction

There are two sources of habitat variability that influence plant species composition in the native temperate grassland vegetation: the natural patterns reflecting large- and small-scale environmental variations and the overlying effects of disturbance.

Large- and small-scale environmental factors

Large-scale environmental variations are driven by moisture availability regulated by air temperature, precipitation, and potential evapotranspiration (Barbour et al. 1980). On a continental scale, the grasslands of central North America clearly reflect a gradient of moisture conditions, with the tall-grass prairie in the wettest region, short-grass in the driest, and the mixed-grass prairie in medium geographic and moisture regions (Sims et al. 1978, Barbour et al. 1980). Similarly, the geographical distribution of major grassland communities within the aspen parkland and adjacent grassland ecoregions in Alberta is controlled by climatically driven moisture availability (Strong and Legat 1992). Fescue grasslands of the aspen parkland occupy the moist end of the gradient, followed by the mixed-grassland at intermediate moisture conditions, and the dry mixed-grass prairie inhabits the dry end of the gradient (Figure 1-1, Chapter 1). In addition, Bowser et al. (1962), Wyatt et al. (1944), and more recently Hogg (1994) and Pettapiece (1995) have suggested that there is a moisture gradient within the aspen parkland of Alberta (Figure 1-2, Chapter 1). According to them, moisture availability increases from southeast toward the northwest portion of the aspen parkland.

On a small scale (, grassland plant species directly compete with each other for available resources, such as light, soil moisture, and soil nutrients. In undisturbed grassland communities, dense stands of dead plant material and live canopy of taller dominant grasses ("competitors", *sensu* Grime (1979), or "species at the top of the competitive hierarchy", *sensu* Keddy (1990a)) cause inadequate light conditions for shorter plants

(Grime 1979). However, the availability of soil water, which also influences the uptake of nutrients by roots, not only depends on competitive abilities of neighboring plants but is also influenced by local topography and soil physical and chemical properties (Barbour et al. 1980).

In the northern hemisphere, south- and east-facing slopes receive higher solar radiation than north- and west-facing slopes; this results in higher evapotranspiration and drier conditions on south- and east-facing slopes (Barbour et al. 1980). On the other hand, soil moisture conditions depend on soil texture and organic matter content. Coarse textured soils (most often rapidly to well-drained soils) have low water-holding capacity compared to medium and fine-textured soils and, therefore, plants growing on sandy soils, in general, experience dry soil conditions (Weaver and Clements 1938). However, high organic matter content in the soil may significantly improve moisture conditions of soils (Naeth et al. 1991c). Plant species that are frequently found on either warm south- and east-facing slopes or on well-drained sandy soils are drought-resistant and chategorized as "stress tolerators" or as "stress-tolerant competitors" (Grime 1979).

Chemical properties of the soil, such as salinity and sodicity, are important characteristics of local soil conditions. Besides their direct toxic effect upon plants, high concentrations of soluble salts interfere with soil water availability by raising the osmotic potential of the soil solution and reducing water uptake by plant roots (Bresler et al. 1982). These soil conditions prevent successful establishment of salt-intolerant species (glycophytes), thereby allowing numerous facultative and obligate halophytic species to grow. On the other hand, in non-saline sodic soils (soils in which sodium represents the main soluble salt), high concentration of sodium salts also have a twofold effect on plants. First, they significantly influence the physical properties of the soil by causing fragmentation of silt particles into clay particles, resulting in low soil permeability to water and air, frequent puddling, and soil hardness during dry periods (Cairns and Szabolcs 1973, Bresler et al. 1982). Those soil conditions limit root penetration and water and air uptake by plants. Second, high sodium concentrations interfere with uptake of other cations from the soil

solution, resulting in magnesium, calcium, and nitrogen deficiencies in plants (Cairns et al. 1962, Toogood and Cairns 1978, Bresler et al. 1982).

Small-scale disturbances

The importance of natural and anthropogenic disturbances for plant species composition and diversity has been increasingly emphasized in recent decades (Sousa 1984, Picket and White 1985, Collins and Glenn 1988). Those reviews have addressed the importance of large-scale disturbance, such as fire, storms, or drought, in different terrestrial and marine ecosystems. Significantly less attention has been given to small-scale disturbances, such as those caused by ungulates, or burrowing animals, in grassland ecosystems. Ungulates (cows, horses, or bison) may have complex effects on species composition by removing vegetation and influencing the nitrogen cycle (Hobbs 1996). A removal of live and dead vegetation lowers the competitive abilities of dominant grasses, thus allowing the invasion of inferior competitors (Weaver and Roland 1952, Harper 1977). The reverse may be true for urine addition (providing readily available nitrogen to the topsoil), which causes a switch in species composition back to a small number of competitive species (Steinauer and Collins 1995). Dormaar et al. (1990) and Dormaar and Willms (1998) reported a significant positive correlation between soil mineral nitrogen and the grazing intensity in fescue grasslands near Stavely, Alberta. Nitrogen directly influences primary and secondary production, and therefore, it is a key element in grassland ecosystems (Dormaar et al. 1990, Steinauer and Collins 1995).

Characteristic species occupy heavily trampled areas, such as livestock paths and farm tracks. Light-demanding and trampling-tolerant species, such as *Poa pratensis*, *Matricaria matricarioides* (Les.) Porter, *Plantago major* L., *Potentilla anserina* L., and *Polygonum arenastrum* Jord. *ex* Bor., are frequent inhabitants of such habitats (Crawley 1986). Other effects of litter removal and trampling by cattle on soil moisture conditions, soil compaction, and soil erosion in fescue grasslands of Alberta (including both *Festuca hallii* in the aspen parkland and *Festuca campestris* in the foothills area) have been extensively reported by Dormaar et al. (1989, 1998), Naeth et al. (1990a, b, 1991a, b, c), and Naeth and Chanasyk (1995, 1996). Burrowing animals, such as bannertail kangaroo

rat (*Dipodomys spectabilis*), badger, and pocket gophers (*Thomomys bottae* or *Geomys byrsarius*) significantly affect the small-scale plant community structure by creating microhabitats of mixed soil, with distinctive light, water, and nutrient conditions (Platt 1975, Inouye et al. 1987, Martensen et al. 1990, Guo 1996). These microsites create habitat heterogeneity that allows the establishment of fugitive species usually absent from undisturbed areas. Fugitive species develop from the persistent soil seed bank brought to the surface by soil mixing (Roberts 1986, Gross 1987) or from wind-dispersed seeds that arrive at the disturbed site (Platt 1975, Martensen et al. 1990, Guo 1996).

Similar effects on soil physical properties and plant composition can be seen on small-diameter pipeline constructions. Relatively new, "environmentally friendly", no-strip treatments result in the removal of native vegetation in a ca. 60 cm wide trench area and mixing of top soil with subsoil, thus, allowing fugitive species to become established (Adams et al. 1996). The authors also reported a loss of up to 75% of the organic matter in the upper 15 cm of the soil profile as a result of soil mixing. However, in salt-affected soils, such as Brown Solod soils, the additional change in affected soils occurred in soil chemistry (Adams et al. 1996). Trenching caused mixing of sodic subsoil (B and C horizons) with chemically neutral topsoil (A horizon), thus significantly increasing the concentration of soluble salts and sodium in the topsoil which persisted for at least two years after the disturbance.

The ability of exotic species to invade native grassland communities

Numerous reviews have related exotic species invasions to environmental conditions. The importance of large-scale climatic conditions, such as the interaction of moisture and temperature, has been suggested by Lindsay (1953), who reported the influence of climate characteristics on the geographical ranges for numerous exotic species in Wisconsin, USA, and surrounding areas, including the Canadian Prairie Provinces. The importance of microclimatic conditions, such as light, soil moisture, and soil nutrients (mainly nitrogen and phosphorus), was discussed by Swincer (1986). The author suggested that, in most cases, both large- and small-scale environmental conditions have to be favorable for exotic plants to become successfully established. Thus, the climatic

and local habitat conditions to which the invader was preadapted in its original habitat may play an important role in the successful invasion of new areas (Swincer 1986). Rejmánek (1989) reviewed numerous studies to relate exotic species invasion to habitat moisture conditions (with no reference to native grasslands) and suggested that mesic habitats are more prone to invasion than xeric or hydric ones.

The invasion of grasslands by exotic species has been associated most frequently with natural or anthropogenic disturbances that create "temporary windows" (*sensu* Johnstone 1986) for invader species to become successfully established (Fox and Fox 1986, Mooney and Drake 1986, and Drake et al. 1989). The relative importance of the large- and small-scale environmental conditions and habitat disturbances for exotic species invasion has rarely been investigated. Mack (1989) and Knops et al. (1995) suggested that despite favorable climatic conditions, exotic species require disturbances to invade natural communities. Therefore, the question is: how much does the susceptibility of the habitat to exotic species invasion reflect a preadaptation of native and introduced species to climatic and local environmental conditions in their original habitats rather than their preadaptation to natural and anthropogenic disturbances?

Grasslands of the Aspen Parkland Ecoregion of Alberta

Grasslands of the Aspen Parkland Ecoregion of Alberta represent the non-treed portion of a ca. 200 km wide transition zone between the main grassland region to the south and the boreal forest to the north (Strong and Leggat 1992). Detailed descriptions of the climate, soils, and vegetation in the aspen parkland were given in Chapter 1. Moss and Campbell (1947) described *Festuca hallii* "virgin" grasslands of the aspen parkland and emphasized that *F. hallii* dominated the undisturbed grasslands to the exclusion of most other grass and forb species. Achuff (1994) recently recognized the Fescue Grassland Subregion within the Grassland Natural Region. It has been suggested that aspen parkland grasslands represent the northern extension of those fescue grasslands from the Grassland Natural Region (Anonymous 1997).

Even the earliest observations of grassland areas within the aspen parkland indicated small-scale variability of species composition in respect to the environmental conditions and disturbances. Moss and Campbell (1947) suggested that the composition of fescue grasslands depended on topography, soil conditions, and herbivory. They recorded a dominance of southern prairie species on very dry, south-facing slopes and an expansion of grazing-tolerant species to overgrazed areas. However, no quantitative data supported their observations. Wroe (1971) and Wheeler (1976) studied two small, relatively undisturbed areas within the aspen parkland (one quarter section of the Rumsey Ecological Reserve and three quarter sections near Kinsella) and their quantitative data on change of species composition in regards to topography, soils, and grazing showed dominance of *Festuca hallii* grasslands on north-facing slopes and the codominance of *Stipa curtiseta* on hilltops and south-facing slopes. They speculated that codominance of *Stipa curtiseta* may have resulted from past grazing, because of observed cattle preference to graze hilltops and south-facing slopes. Coupland and Brayshaw (1953) reported the dominance of *Festuca hallii* grasslands in the northern portion of the aspen parkland in Saskatchewan and the codominance of *Stipa curtiseta* within the southern fringe of the area. The last study suggested that species composition in grasslands of the aspen parkland may respond to a variation in the large-scale climatic conditions.

Heavy grazing and anthropogenic disturbances, such as road rights-of-way, powerlines, and pipelines, create conditions that may increase the loss of native species and the invasion by exotic ones in grasslands of the aspen parkland (Anonymous 1997). Limited information from different areas in the aspen parkland of Alberta suggested a positive relationship between exotic species invasion and anthropogenic disturbances (Bork 1993, Achuff 1990). In addition, in their historical reviews, Bird (1961) and North (1976) suggested that the alteration of native plant communities by cattle grazing in aspen parkland has caused changes in the composition of burrowing animal species, which in turn influenced changes in the native flora. Many aspects of ecological importance of uninvaded, diverse native plant communities in remnant prairie grasslands of the aspen parkland have been discussed in Chapter 1. In addition, studies on *Festuca campestris* grasslands near Stavely, Alberta, found significantly higher production in native fescue

pastures than in ones heavily invaded by *Poa pratensis* (Willms et al. 1996). However, no attempt has been made to evaluate quantitatively the relative importance of the large- and small-scale environmental factors and small-scale disturbances (including grazing) on plant species composition and exotic species invasion in remnant fescue grasslands across the aspen parkland in Alberta.

Objectives

The objectives of this part of the study were (1) to determine small-scale (1 m^2) vascular plant species composition in a number of remnant fescue grasslands within the aspen parkland, and to relate composition to the large (regional)- and small (1 m^2)-scale environmental conditions and overlying disturbances; (2) to determine the relative importance of large- and small-scale environmental factors and overlaying disturbances for exotic vascular plant species invasion; and (3) to suggest what model best describes the assembly of vascular plant species in fescue prairie grasslands along disturbance and environmental gradients.

Methods

Field sampling

Sampling of vegetation and environmental data in 490 quadrats was conducted from July 14th to August 20th 1996, when most species were phenologically well developed. Although all quadrats had an area of 1m^2, the actual shape of the quadrat depended on the type of the disturbance sampled (e.g., on a cow path and under a fence, the quadrat was elongated as much as 2 m × 0.5 m). At each quadrat, percent cover of vascular plants, mosses, and lichens was visually estimated to the nearest 1%. A plastic frame of 1 m^2 sub-divided into 100 smaller quadrats of 100 cm^2 areas aided the visual estimation. For species that covered less than 1% of the quadrat, 0.1% cover values were assigned. Nomenclature followed Moss (1983) for vascular plants, Ireland *et al.* (1987) for mosses, and Esslinger and Egan (1995) for lichens. For *Festuca hallii* and *F. campestris*, nomenclature followed Pavlick and Looman (1984). Identification of some species without flowers (*Antennaria*), leaves (*Rosa*) or sporophytes (*Brachythecium*) was impossible, thus, only the genus was noted for these plants.

The height of the standing litter and the depth of the fallen litter were measured as an indicator of disturbance because they influence light conditions (Willms and Quinton 1995) and the micro-site moisture regime (Naeth *et al.* 1991b). Litter refers to all intact dead organic material above the mineral soil. Percent cover of exposed mineral soil was visually estimated to the nearest 1% as an indicator of disturbance. Slope and aspect were recorded for the later estimation of average annual solar radiation. At the center of each plot, one block of soil (15 cm × 15 cm and 25 cm deep) was collected for soil analyses. The depth of the soil cores was chosen based on the data provided by Coupland and Brayshaw (1953) on the weight of roots of three dominant grasses within the aspen parkland: *Festuca*, *Stipa*, and *Koeleria*. Their data show that 73.4, 71, and 66.7% of the root weight of these species occurs within the top 15 cm of soil, with an additional 12, 18.4, and 16.5%, respectively, occurring within the underlying 15 cm. Therefore, 25 cm should contain about 85, 89, and 83% of the root weight.

Laboratory analyses

Air-dried soil samples were ground to pass through a 2 mm sieve. The saturation paste method was used for the analysis of soluble cations (Ca^{2+}, Mg^{2+}, Na^{+}) and for electrical conductivity (EC) measurement (McKeague 1978). Soluble Ca^{2+} and Mg^{2+} were determined on a Perkin-Elmer atomic absorption spectrophotometer (Model 503, Perkin-Elmer Norwolk). Flame emission on the same instrument was used to determine soluble Na^{+}. The sodium adsorption ratio (SAR), a measure of soil sodicity, was calculated from Ca^{2+}, Mg^{2+}, and Na^{+} according to Richards (1954). The exchangeable sodium percentage (ESP), an alternative to SAR, has been used extensively in the literature instead of SAR to identify sodic soils and plant species tolerance to sodic conditions. Levels of ESP between 10% and 15% should be considered potentially detrimental to plants (Bresler et al. 1982). Since the direct measurement of ESP is costly and time-consuming (Bresler et al. 1982), estimations can be made from SAR by employing a simple mathematical formula (Richards 1954). However, Bresler et al. (1982) suggested that SAR should be used as the main criterion for excessive soil sodium levels (ESP of ca. 15% is equivalent to SAR of ca. 13). Electrical conductivity was determined on a conductivity bridge

instrument (Model 31, Yellow Spring Instrument Co., Inc.) and is a measure of soil salinity. Soils are considered saline if the EC reaches values of 4 dS/m or higher (Richards 1954). Mineral nitrogen (sum of NH_4-N, and NO_3-N) was determined using a Technical Autoanalyser II (Technical Industrial Systems). After grinding soil samples to pass through a 0.15 mm sieve, organic carbon (OC) was measured by the Walkly-Black method (Walkly and Black 1934). Soil organic matter refers to the organic fraction of mineral soil and can be calculated by multiplying the value for organic carbon by an appropriate coefficient. For the purposes of this study, values for organic carbon were used instead of organic matter. Soil texture (percent of total clay, silt, and sand) was measured according to the hydrometer method of Sheldrick and Wang (1993).

Data analyses

Three different clustering methods were employed to obtain the best clustering of quadrats. TWINSPAN is a polythetic divisive method of classification (Hill 1979, Kent and Coker 1992). It clusters both quadrats and species and constructs a two-way table from a quadrat-by-species matrix. It assumes that each group of quadrats can be characterized by a group of species that prevail in one side of the dichotomy (differential species). Since the idea of differential species is of a qualitative nature, quantitative data (e.g., % cover) are first replaced with the qualitative equivalent. This equivalent is the "pseudospecies". Any species-abundance scale is being partitioned into a series of "pseudospecies" similar to a crude scale, such as the Braun-Blanquet scale of cover-abundance (Muller-Dombois and Ellenberg 1974). The levels of abundance that are used in TWINSPAN to define the scale are called "pseudospecies cut levels" and are defined by the user. Three different "pseudospecies" cut-levels were used in this study: 0, 2, 5, 10, 20 (the default); 0, 2, 5, 10, 20, 50; and 0, 2, 5, 10, 20, 50, 75. TWINSPAN then proceeds with the ordination of samples via correspondence analysis (Hill 1973) and a crude division into negative and positive sides of a dichotomy. Subsequent dichotomies are constructed by using frequencies of the species on the positive and negative sides. Detailed procedures of clustering of species and quadrats and the construction of a species-by-quadrats table are given in Jongman et al. (1987).

The remaining two clustering methods employed use a hierarchical agglomerative clustering that proceeds from individual samples or quadrats and progressively combine them based on their similarity until all samples are in one group (similarity analysis). Dissimilarity (D) is the complement of similarity (S) in that

$$D=1-S$$

From more than 20 similarity/dissimilarity measurements available, the Bray-Curtis dissimilarity coefficient was chosen to obtain a dissimilarity matrix (Legendre and Legendre 1983). Bray-Curtis coefficient is a semimetric that uses data on species abundance to calculate the distance between samples. The formula for the Bray-Curtis coefficient is

$$D_{(i,j)} = \Sigma |X_{ik} - X_{jk}| / \Sigma (X_{ik} + X_{jk})$$

where $D_{(i,j)}$ represents the percentage difference between quadrats i and j, X_{ik} is the value of species k for quadrat i, and |X| means the absolute value of quantity X. The feature of that distance measure is that a set difference contributes the same amount to the distance, whether it occurs between rare or abundant species. Bloom (1981) emphasized the ability of the Bray-Curtis distance measure to detect accurately the true resemblance along the entire range of species abundances. Two agglomerative clustering methods used in this study were Unweighted and Weighted Arithmetical Average Clustering (UPGMA and WPGMA, respectively). In the computation of the arithmetic average for two clusters, UPGMA gives equal weights to all objects. It may cause a bias when a large cluster of quadrats of common origin are to be combined with a much smaller cluster of quadrats. WPGMA corrects for that bias by giving equal weights to both clusters being merged whatever their size (Legendre and Legendre 1983). This procedure provides a sharper contrast to the classification. After the initial clustering, 11 quadrats were excluded from the analyses because they produced clusters made up of only one or two quadrats.

In order to relate plant species composition of quadrat clusters to the underlying environmental factors, a direct gradient analysis was performed (Whittaker 1967, Whittaker 1978). The preference for direct over indirect gradient analysis has been discussed in a number of publications (Legendre and Legendre 1983, Keddy 1991, Kent and Coker 1992). Environmental data collected from 11 remnant areas by stratified

randomization provided a spatially discontinuous gradient (Keddy 1991), which can be used for a direct gradient analysis. The complexity of topographic and other environmental factors in space make the plant community pattern complicated and the relationships between plant species composition and underlying environmental factors obscure. Direct gradient analysis "disentangles" that spatially complex relationship and shows how patterns of species composition relate to environmental variables (Whittaker 1978). Canonical Correspondence Analysis (CCA) was used to relate environmental variables to the plant species composition (ter Braak 1986, 1994). This multivariate technique is an extension of Correspondence Analysis (CA), with the restriction that canonical axes that are linear combinations of environmental variables replace axes from CA. Canonical correspondence analysis includes a multiple regression of the original quadrat scores on the environmental variables during the algorithm. Therefore, CCA performs environmentally constrained ordinations of quadrats and species. Canonical correspondence analysis was performed by CANOCO 3.1 (ter Braak 1988, 1990).

Two CCA analyses were performed to evaluate the importance of environmental and disturbance variables in determining plant species composition. Thirteen variables (Table 2-1) were included for the first CCA (CCA-1). Those included four disturbance variables (standing and fallen litter, organic carbon, and exposed mineral soil), seven small-scale environmental variables (mineral nitrogen, sodicity, salinity, sand, silt, clay, and solar radiation), and the large-scale environmental variables (longitude and latitude). There were two reasons to represent large-scale environmental variable (mainly climatically driven moisture) by a geographical position determined by longitude and latitude. Firstly, the precise information on moisture indices for the two southern sampling regions, Rumsey and Wainwright (Figure 1-2, Chapter 1), was not available, and the substitution by spatial variables would reflect general moisture conditions more accurately than the extrapolation of moisture indices. On the other hand, two spatial variables provided an opportunity to identify relationships between geographical location of remnants and small-scale environmental variables (spatially structured environmental variables). Those two terms, large-scale environmental variable(s) and spatial variables will be used

interchangeable for the remainder of this chapter. Mean annual solar radiation was calculated from latitude, slope, and aspect data using the Bonan method (Bonan 1989).

The two spatial variables (latitude and longitude) have been excluded from the computation in the second CCA (CCA-2) to examine the importance of local environmental variables (including disturbance variables) alone. The default provided by CANOCO has been modified in the same way in both CCA's in order to improve the analyses. After initial ordination, six quadrats and one species were indicated to be extreme outliers; these were removed from further analysis. The SILT environmental variable was made passive, because of the high covariance with another variable (SAND). Downweighting of rare species was used because quadrats with rare species were distorting the analyses. Complete removal of rare species from the analysis can often improve the ordination (ter Braak 1986). Exclusion of 118 species that were considered rare in this study, based on presence in less then 5% of the quadrats, increased percent variance explained, but decreased the explanatory ability of the ordination by decreasing eigenvalues significantly. Thereby, all species except one have been retained in the analyses. Attempts to transform species data by logarithms [$y' = \ln (y + 1)$], as suggested by ter Braak (1987b), to correct for the large number of zeroes in the data set, failed to improve the analysis (based on percent variance explained), and was therefore abandoned.

Three more CCA analyses were performed in order to partition the variation of species abundance data into four independent components: non-spatial environmental (including disturbance), pure spatial, spatially structured environmental, and undetermined. In the first ordination of species and quadrats, species abundance data were constrained by the extended matrix of geographical coordinates only (Legendre 1990, Borcard *et al* 1992). The remaining two CCAs were performed as a partial ordination using the covariable option available in CANOCO 3.1, which allows for an evaluation of the effects of selected variables, while the effects of the covariables on the ordination are removed. Thus, the second CCA determined the importance of the four disturbance and six small-scale environmental variables after the effects of spatial variables had been removed,

while the third CCA evaluated the importance of the geographical position after the removal of the effects of the other ten variables. The detailed procedure for the calculation of the amount of explained variation by each of the components (spatial only, non-spatial, and spatially structured environmental) has been given in Borcard *et al.* (1992) and in Legendre (1990).

Mean values for significant variables defined by CCA-1 and CCA-2 were calculated for all quadrat groups found by the UPMGA and plotted against quadrat groups derived by UPMGA to observe a pattern of change.

Results

Vegetation description

The total number of vascular plant species observed in this study was 205 of which 31 exotic species represented 15% of the total number. In the non-vascular flora, 17 moss species and 27 lichen species were identified. All scientific names for vascular and non-vascular plant species with associated six-letter codes are listed in Appendix 1.

All of the analyses performed by the TWINSPAN clustering program failed to cluster the majority of undisturbed or lightly disturbed quadrats characterized by significantly high cover (50-95%) of late successional species, *Festuca hallii*, and by low species richness. The result from the most successful analysis (grouping the least disturbed quadrats) showed one cluster at the 77th division, containing 50 quadrats. Therefore, after initial attempts to cluster quadrats by TWINSPAN and identify indicator and preferential species, these analyses were abandoned.

Two agglomerative clustering methods provided similar results; therefore, results obtained by UPGMA (a more simple method) have been used to relate vegetation composition on the small scale to environmental variables. Classification of 479 quadrats reflected the complexity of environmental factors and plant community composition in the remnant grasslands of the aspen parkland. A cut at 0.725 (Bray-Curtis distance coefficient) revealed 19 distinct quadrat groups (Figure 2-1). All constant (indicator)

species, frequent species (occurring in more than 70% of the quadrats), and common species (occurring in at least 50 % but less then 70% of the quadrats) with the mean percent cover for quadrats where they occur are listed in Table 2-2. Although non-vascular plants were not included in these cluster analyses, mean percent cover for quadrats where each species occurs has been calculated for all 19 groups. These are presented in Table 2-3.

Floristic characteristics of 19 quadrat groups

GROUP A. Quadrats in this group are dominated by the late successional species *Festuca hallii* with a mean cover of 73.8%. Only one species, *Achillea millefolium* L., is frequently present in the quadrats of group A. In addition, *Stipa curtiseta* and *Anemone patens* L. occur in about half of the quadrats. The majority of 117 quadrats in the group belong to ungrazed and lightly grazed sampling areas.

GROUP B. Group B is characterized by co-occurrence of two of the most abundant species, *Festuca hallii* and *Stipa curtiseta* with mean covers of 12.9% and 19.8%, respectively. *Achillea millefolium*, *Agropyron trachycaulum* var. *unilaterale* (Cassidy) Malte, and *Solidago missouriensis* Nutt. are frequently present. In addition, *Artemisia frigida*, *Carex obtusata* Lilj., *Rosa* spp., and *Koeleria macrantha* occur in about 50% of the quadrats. The 50 quadrats in this group were mainly in areas of medium grazing.

GROUP C. Group C includes quadrats characterized by a high frequency of *Danthonia californica, Festuca hallii, Antennaria* spp., *Stipa curtiseta, Achillea millefolium*, *Agrostis scabra* Willd., and *Aster ericoides* L., none of which cover large area of each quadrat. *Carex obtusata*, *Agropyron trachycaulum* var. *unilaterale*, and *Cerastium arvense* L. are present in about half of the quadrats. The 31 quadrats in this group were medium to heavily grazed.

GROUP D. Sixteen quadrats in this group are characterized by the presence of *Festuca hallii* at each quadrat with a mean group cover value of 6.9%. *Achillea millefolium*, *Agrostis scabra*, and *Vicia americana* Muhl. were present in more than 70% of the

quadrats while *Taraxacum officinale* Weber occurred in about half of the quadrats. Quadrats were from areas that were either heavily grazed or had heavy soil disturbances (top soil removal, soil mixing).

GROUP E. Only five quadrats comprise group E. They are dominated by *Juniperus horizontalis* Moench, and *Festuca hallii* is found in all quadrats with a 19.3% mean cover. Frequently occurring species include *Anemone patens* and *Artemisia frigida*. Quadrats were from medium grazed areas or areas with soil erosion. These five quadrats belong to only two remnants from the Wainwright area.

GROUP F. These quadrats are characterized by the dominance of *Selaginella densa* Rydb. and the constant presence of *Stipa curtiseta* at a smaller abundance. *Festuca hallii*, *Artemisia frigida*, *Carex pensylvanica* Lam., and *Koeleria macrantha* are present in more than 70 % of the quadrats. The majority of the 28 quadrats in this group were moderately to heavily grazed.

GROUP G. The 30 quadrats in group G are similar to quadrats in group F from which they differ mainly by the absence of *Selaginella densa*. In addition, *Bouteloua gracilis* (HBK) Lag. and *Antennaria* spp. are present in the majority of these quadrats. Quadrats were from areas with moderate to heavy grazing.

GROUP H. Group H is characterized by the dominance of the shrub *Symphoricarpos occidentalis* Hook. Species frequently found on these quadrats include *Artemisia frigida*, *Bouteloua gracillis*, *Koeleria macrantha*, and *Stipa curtiseta*. *Festuca hallii*, *Achillea millefolium*, *Antennaria* spp., and *Potentilla concinna* Richards. were present in at least half of the quadrats. These nine quadrats were grazed at medium or high intensities.

GROUP I. Eleven quadrats comprise a group characterized by the consistant presence of *Artemisia frigida* with a mean ground cover of 19.3%, the frequent occurrence of *Stipa curtiseta*, and the presence of *Axyris amaranthoides* L. in half of the quadrats. These quadrats are heavily grazed or are highly disturbed (soil mixing, cow path).

GROUP J. *Poa pratensis* L. dominates in 37 quadrats at the exclusion of most other grass species, except for *Agropyron smithii*. *Aster ericoides*, *Achillea millefolium*, and *Taraxacum officinale* are frequently found forbs in these quadrats. Most of the quadrats were on heavily grazed areas, but some quadrats had mixed soil.

GROUP K. The co-occurrence of *Taraxacum officinale* and *Poa pratensis* characterizes group K's 28 quadrats. The frequently present *Trifolium repens* L. obtains the highest percent cover (23.3%) with *Achillea millefolium* being another frequently occurring species. Heavy grazing, high soil compaction, or soil erosion characterized these areas.

GROUP L. *Poa pratensis* is the only constant species for this group. Frequently occurring species include *Solidago missouriensis* and *Stipa viridula* Trin., whereas *Agrostis scabra*, *Bouteloua gracillis*, *Carex pensylvanica*, *Psoralea argophyla* Pursh, *Potentila concinna*, *Artemisia frigida*, *Agropyron trachycaulum* var. *unilaterale*, and *Stipa curtisera* occur at lower frequencies. All nine heavily disturbed (cow paths, soil mixing) quadrats were in two remnants from the Wainwright region.

GROUP M. Thirty two quadrats of group M are characterized by high frequencies of *Achillea millefolium*, *Aster ericoides*, *Cerastium arvense* L., *Agrostis scabra*, and *Koeleria macrantha*, none of which cover a significant area of each quadrat. Species occurring in more than half of the quadrats but at lower frequencies include *Muhlenbergia richardsonis* (Trin.) Rydb., *Grindelia squarrosa* (Pursh) Dunal, *Agropyron smithii*, *Stipa curtiseta*, *Carex obtusata*, *Solidago missouriensis*, and *Taraxacum officinale*. When present, *Carex obtusata*, *Grindeli squarrosa*, and *Muhlenbergia richardsonis* have the highest percent cover (means are 10.7, 7.8 and 8.0%, respectively). Heavy grazing and soil disturbances characterize this group.

GROUP N. High frequencies of *Agropyron smithii* and *Artemisia frigida* as well as the presence of *Agrostis scabra*, *Bouteloua gracillis*, *Grindelia squarosa*, and *Carex stenophylla* Wahl. in more than a half of the 14 quadrats characterize group N. When present, *Agropyron smithii* and *Carex stenophylla* are the most abundant species (mean

covers are 21 and 12%, respectively). Quadrats in this group occur in heavily grazed and highly disturbed areas.

GROUP O. This group includes 19 quadrats characterized by the presence of *Trifolium repens*, and high frequency of *Achillea millefolium*, *Agropyron trachycaulum* var. *unilaterale*, *Poa pratensis*, and *Solidago spathulata* DC. *Carex sicata* Dewey, *Rumex acetosella* L., *Artemisia campestris* L., and *Campanula rotundifolia* L. are present in more than a half of the quadrats. None of the species had significantly high cover velues. All quadrats were sampled in Elk Island National Park on coarse, sandy soils. Sampled areas are characterized by medium to heavy grazing or by other high soil disturbances.

GROUP P. All 18 quadrats in this group have been highly disturbed and are low in species richness. *Artemisia frigida* is the only frequent species, while *Chenopodium album* L., *Monolepis nuttalliana* (Schultes) Greene, *Polygonum arenastrum* Jord. *ex* Bor., and *Stipa curtiseta* occur in half of the quadrats. None of the species cover more than 2% of the quadrat areas.

GROUP Q. The constant occurrence of *Bromus inermis* ssp. *inermis* characterizes nine quadrats in group Q. Although not frequent, *Artemisia frigida*, *Melilotus alba* Desr., and *Polygonum arenastrum* occur in different combinations. Quadrats were either heavily grazed or even more highly disturbed and were located in two remnants from the Wainwright region.

GROUP R. These six heavily disturbed quadrats were dominated by *Lepidium densiflorum* Schrad. *Agropyron smithii* is frequent, while *Stipa curtiseta*, *Agropyron trachycaulum* var. *unilaterale*, *Bouteloua gracilis*, and *Chenopodium album* are present in half of the quadrats.

GROUP S. The constant occurrence of *Taraxacum officinale* and the presence of *Polygonum arenastrum*, *Agropyron repens* (L.) Beauv. and *Puccinellia distans* (L.) Parl. in different combinations characterize these ten highly disturbed quadrats.

Canonical Correspondence Analyses

Using all variables (CCA-1), the first four axes explain 9.0% of the variation in the species data set (Table 2-4). The relative magnitude of the eigenvalues (λ) for the first four canonical axes and ratios between them, indicate that the first two axes are the most important for the interpretation of the ordination of 484 quadrats and 204 species along 12 environmental variables. The highest eigenvalue of the first axis shows that the highest percentage variance in the species data is accounted for by that axis. Relatively small decrease in the magnitude of the second eigenvalue ($\lambda 1/\lambda 2 = 1.6$) indicates that the vegetation groups are influenced by environmental gradients, which form at least two (complex) gradients represented by first two axes.

The species/environmental correlation is a measure of the relationship between the quadrat scores resulted from weighted averaging from a CA and those calculated from a CCA (ter Braak 1988). High correlation indicates that a high proportion of the species data is explained along that axis. On the contrary, when environmental variables fail to explain adequately the variation along an axis, the correlation value is low, resulting in the distortion of the ordination. The first two axes have relatively high ($r = 0.83$ and 0.73) species/environmental correlations, while axes three and four have lower correlations ($r < 0.7$) (Table 2-4). Low eigenvalues and low species/environmental correlations for axes three and four indicate that they do not significantly explain the relationship between plant composition and environmental variables at the scale chosen in remnant grasslands.

Cumulative percent variance in the weighted averages of the species with respect to each of the environmental variables for the first two axes is 54.5 (Table 2-4) and has to be taken into account when interpreting species and quadrat biplots for the first two axes (ter Braak 1987a). Axes three and four add only 18.9% to the variance of species/environmental relation that has already been accounted for by the first two axes (Table 2-4).

Based on the canonical coefficients and inter-set correlations (ter Braak 1988), fallen litter and standing litter are the most important variables defining Axis 1, followed by

exposed mineral soil and organic carbon (Table 2-5). Fallen litter, standing litter, and organic carbon vary in opposite direction from exposed mineral soil. Quadrats on the right side or the ordination generally have higher fallen and standing litter along with the higher soil organic carbon, and they are low in exposed mineral soil (undisturbed or lightly disturbed). On the other hand, quadrats toward the left end of the first axis are generally disturbed to higher degrees than the previous ones, and, therefore, they tend to have lower values for standing and fallen litter and organic carbon. Although significant, solar radiation and sand have smaller explanatory values for the first axis.

Longitude has the highest correlation with Axis 2, followed by mineral nitrogen, latitude, and percent of total sand (Table 2-5). Total clay, solar radiation, and exposed mineral soil have lower correlations than the previous variables, but all have significant correlations and important canonical coefficients with this axis. Mineral nitrogen, latitude, total clay, and exposed mineral soil increase in the opposite directions of longitude, total sand, and solar radiation. Quadrats on the upper end of Axis 2 are generally found on soils with medium to fine soil texture, which are often higher in mineral nitrogen. These quadrats are also associated with the northwestern part of the ecoregion and they do not constitute areas with high solar radiation. At the opposite (negative) end of Axis 2, quadrats are generally exposed to higher solar radiation and/or are associated with sandy soils. In addition, quadrats positioned along the negative end of Axis 2 may also be from areas located more toward the southeast compared with quadrats along the positive end of this axis. Soils, which support vegetation on quadrats along the negative end of Axis 2, are generally low in mineral nitrogen.

When only ten micro-site environmental variables were used in CCA (CCA-2), the results were similar to those obtained by inclusion of the geographical position. The first four axes explain only 7.9% of the variation in the species data set (Table 2-6). While the first ordination axes has the same eigenvalue as in CCA-1, the eigenvalue for the second canonical axes is somewhat lower (λ=0.24). The species/environmental correlation for the first two axes is similar as in the first CCA (0.82 and 0.70, respectively). Axes three and four have again low correlations ($r<0.7$). Cumulative percent variance in the

weighted averages of the species in respect to each of the environmental variables for the first two axes is higher in CCA-2 (60.4) (Table 2-6).

Statistics for the environmental variables used in CCA-2 differ from those obtained by CCA-1 mainly in the importance of the environmental variables, whose linear combination defines the second axis (Table 2-7). While mineral nitrogen, total sand, solar radiation, and exposed mineral soil show similar patterns as in CCA-1, the sodium adsorption ratio has the highest significant correlation and an important canonical coefficient with this axis. This variable increases in the same direction as mineral nitrogen, indicating that quadrats arranged along the positive end of Axis 2 may contain species adapted to moderate to high sodic soils.

The sums of canonical eigenvalues were the only results from three additional CCA analyses used to partition the variation between spatial and non-spatial environmental components of the ecological variation. The second CCA (CCA-2) and three additional CCA analyses provide the following global results: (1) CCA of the species matrix constrained by the environmental/disturbance matrix of ten variables (geographical coordinates excluded): sum of all canonical eigenvalues = 1.045; (2) CCA of the species matrix constrained by the extended matrix of geographical coordinates only: sum of all canonical eigenvalues = 0.613; (3) the same as (1), after removing the effects of the geographical matrix: sum of all canonical eigenvalues = 0.860; and (4) the same as (2), after removing the effects of the environmental/disturbance variables: sum of all canonical eigenvalues = 0.428.

The sum of all unconstrained eigenvalues (total inertia) of the species matrix derived by correspondence analyses (CA) was 10.386. Thus, the percentage of the total variation of the species matrix accounted for by non-spatial environmental/disturbance, spatial, and spatially structured environmental/disturbance component is 8.28, 4.12, and 1.78% respectively (Table 2-8). Thus, 85.8% of the variation in the abundance data for 204 species is considered unexplained.

Distribution of vascular plant species on the CCA-1

Species scores from CCA-1 based on all 12 variables have been used to relate vascular plant species to the underlying environmental and spatial factors. When only indicator, frequent, and common species from 19 groups derived by UPGMA have been plotted, the ordination shows a clear division between late successional species (*Festuca hallii*) on the positive end, and the majority of the species on the negative end of Axis 1 (Figure 2-2). The second axis represents a clearer division between native and exotic species. Native indicator (constant) species are arranged near the negative end of the axis, while exotic indicator and common species are scattered near the opposite end of the axis. Frequent native species are mostly situated around the origin of the axes on the positive end of Axis 2. Common native species do not show a clear pattern.

When indicator species for dry conditions are displayed on the ordination diagram, they clearly show the preference toward the negative end of the first axis (Figure 2-3). The majority of species is located along the negative end of the second axis, whether they indicate sandy or otherwise dry soil conditions There are only 3 exotic species collected during the study that are known to occur predominantly in dry or sandy conditions. These were *Salsola kali* L., *Tragopogon dubius* Scop., and *Agropyron pectiniforme* R. & S.

As indicated in Figure 2-4, species of moist to wet soil conditions mainly align along the positive end of Axis 2, while the majority of plant species are concentrated at the middle of Axis 1. Figure 2-5 displays plant species that are known to exhibit tolerance for moderate to high sodicity or saline soil conditions. The majority of species are found at the negative end of the Axis 1 and at the positive end of Axis 2. Figure 2-6 shows plant species that are often related to disturbed soils. The majority of these species are found near the negative end of the Axis 1 and at the positive end of Axis 2. Exotic and native species are equally represented; however, exotic species show a somewhat stronger tendency toward the positive end of Axis 2 than native ones. Annual plant species show a clear position at the negative end of Axis 1 and at the positive end of Axis 2 (Figure 2-7), whereby the number of native annual species is almost equal to the number of exotic ones.

Distribution of quadrat groups derived by UPGMA *on the* CCA-1

When quadrat scores have been used to plot quadrats on the ordination diagram based on CCA-1, quadrat group A shows a clear restriction to the positive end of Axis 1. An equal number of quadrats exists along both ends of Axis 2 (Figure 2-8). There is considerable overlap of the quadrat groups on the ordination diagram on both ends of Axis 2. Quadrat groups B, E, F, G, H, L, and Q radiate toward the negative ends of both axes (Figures 2-9, 2-12, 2-13, 2-14, 2-15, 2-19, and 2-24). Quadrats from groups C, D, I, J, K, M, N, O, P, R, and S are mainly arranged at the negative end of Axis 1 and positive end of Axis 2 (Figures 2-10, 2-11, 2-16, 2-17, 2-18, 2-20, 2-21, 2-22, 2-23, 2-25, and 2-26). When quadrats from each region (Elk Island National Park, Kinsella, Wainwright, and Rumsey) have been assigned a different symbol, an identical pattern can be observed on most of the figures. Quadrats from the same geographical region tend do be clustered with respect to the Axis 2. In addition, quadrats from Elk Island National Park region radiate toward the positive end of Axis 2 in respect to the quadrats from the other three regions, while quadrats from the Wainwright area occupy opposite end of the "cloud" formed by all quadrats of the group. Quadrats from Kinsella and Rumsey region usually occupy median position in respect to the quadrats from the other two regions.

Pattern of the mean values for significant variables for 19 quadrat groups

Distinct trends of the decrease of fallen litter and increase of exposed mineral soil are apparent throughout the UPGMA quadrat groups starting with the undisturbed or lightly disturbed quadrat group A (Figure 2-27a, c). Sharp decreases in standing litter with the disturbance higher than light grazing is clear from Figure 2-27b. Negative correlations between organic carbon (OC), fallen litter, and standing litter on one side, and exposed mineral soil on the other, indicated by both CCA-1 and CCA-2, are shown on Figure 2-27a-d. Negative correlations between mineral nitrogen and total clay on one side and total sand on the other, indicated by both CCA-1 and CCA-2, is shown on Figure 2-27e, f, h. Sodicity is most often low in sandy soils, and its mean reaches a value above 10 in only six quadrat groups toward the right side of Figures 2-27g. Solar radiation with means higher than 700 KJ/cm^2 represent quadrats from warm south or southeast facing slopes (Figure 2-27i). Only five quadrat groups (E, K, L, O, and Q) show a relatively narrow

geographical location of quadrats (Figure 2-27j, k). Quadrats from other 13 groups do not show a clear preference toward a geographical region.

Finally, direct gradient analysis showed that for only 39 out of 204 plant species did the percentage of variation per species explained exceed 10%, being the highest for *Festuca hallii* (63.41%) (Table 2-9).

Discussion

What did cluster analysis and group mean values for environmental and disturbance factors say about plant species composition at the small scale?

The high number of quadrat groups (19) derived by cluster analysis (Table 2-2) and the mean values for variables (spatial, environmental, and disturbance) for each quadrat group (Figure 2-27) reflected the complexity of habitat characteristics underlying the plant species composition at the 1 m^2 scale. However, distinct gradients of three indicators of disturbance, fallen and standing litter and exposed mineral soil, were evident throughout the quadrat groups (Figure 2-27a, b, c). Examination of indicator, frequent, and common plant species characterizing each quadrat group showed that quadrats with higher standing and fallen litter and lower percent of exposed mineral soil were characterized by the presence of the late successional species *Festuca hallii* at different abundances, and by the low frequency and abundance of exotic species (quadrat groups at left end of Table 2-2). In addition, one quarter of all quadrats (117) belonged to a single cluster characterized by the strong dominance (mean cover = 73.8 %) of *Festuca hallii*, high frequency of *Achilea millefolium*, and the presence of only two other species, *Stipa curtiseta* and *Anemone patens*, in more than half of the quadrats (quadrat Group A in Table 2-2). These quadrats were characterized by the highest standing and fallen litter, and the absence of exposed mineral soil (Figure 2-27a, b, c), and were mostly undisturbed or lightly grazed only.

The foregoing results suggest that disturbances, which result in the removal of especially standing litter, are required for the majority of plant species to invade fescue grasslands of the aspen parkland. This agrees with previous observations by Moss and Campbell

(1947), Coupland and Brayshaw (1953), Wroe (1971), and Wheeler (1976) who reported the dominance of *Festuca hallii* in undisturbed grassland areas to the exclusion of other species. Somewhat contrasting results from Saskatchewan aspen parkland reported by Coupland and Brayshaw (1953) and Coupland (1961) in regards to the percent cover by *Festuca hallii* in relatively undisturbed sites (maximum 40-50% and 36.3-43.1%, respectively) probably reflected the difference in the sampling methods. Later studies used the point method and measured basal areas as opposed to the visual estimated cover used by Moss and Cambell (1947), Wroe (1971), Wheeler (1976), and in the present study. Species that grow in relatively small clumps show aerial vegetative growth that often greatly exceeds the actual ground space occupied by the plants (Shimwell 1971). Clumps of *Festuca hallii* are between 7 and 10 cm in diameter and are up to 80 cm tall (Pavlick and Looman 1984), therefore it is likely that a measure of the basal area will underestimate the total cover by the aerial vegetative growth. Weaver and Clements (1938) suggested that leafy shoots of the crown are a better measure of competition for light in grasslands, thereby justifying using a visual estimation of the aerial vegetation growth.

Festuca hallii produces a thick and persistent litter when undisturbed (Gerling et al. 1995). Shading by litter cools the ground and, helped by high water holding capacity of the accumulated organic matter, suppresses evapotranspiration. This results in better soil moisture conditions early in the growing season, particularly at depths below 30 cm (Naeth *et al.* 1991a). The increase in organic matter and moisture in soils under ungrazed stands of *Festuca campestris* near Stavely, Alberta, were reported by Johnson (1961) and Dormaar et al. (1989). Although similar data are not available for Alberta's grasslands, studies from Saskatchewan sites showed that ca. 15% of the root weight of *Festuca hallii* extended deeper than 30 cm in the soil (Coupland and Brayshaw 1953), thus allowing this species to reach more deeply stored water once water reserves diminish from the upper soil layers. Because *Festuca hallii* is a C_3 grass that achieves the best growth early in the season (Anderson and Bailey 1980), it benefits from improved soil moisture conditions in the spring. Standing live crop and dense standing litter of relatively tall plants deny light to shorter competitors and to ones that grow later in the season (C_4

grasses) and reduces their ability to forage for nutrients (Keddy 1990a). Accumulation of litter reduces germination and survivorship of seedlings and other small plants (Bergelson 1990, Tilman and Wedin 1991, Tilman 1993). Consequently, it seems that early growth and production of heavy litter make *Festuca hallii* a strong competitor (*sensu* Grime 1979) that, when undisturbed, competes successfully with other species and significantly decreases species richness.

On the other hand, the absence of *Festuca hallii* from quadrats with low fallen litter and high percent of exposed mineral soil is not surprising since these quadrats have been exposed to higher disturbances, including heavy grazing, mixing of soil and different levels of topsoil removal. Sensitivity of the closely related *Festuca campestris* to heavy grazing has already been documented (Willms et al. 1985, Dormaar et al. 1989). The data are not available for mixed soil resulting from animal burrowing or removal of different soil horizons; however, observations of similar disturbances, such as small diameter pipeline constructions without re-seeding in the Rumsey Ecological Reserve, indicated that close to ten years of succession without disturbance (or with mowing only) is required for the re-invasion of *Festuca hallii* from adjacent undisturbed areas (Barry Cole, personal communications).

Similarly, the higher frequency and abundance of exotic species in quadrats with higher exposed mineral soil resulting from heavy grazing and trampling or removal of topsoil is in agreement with previous reports from the aspen parkland. Bork (1993) reported the heavy invasion of exotic species, such as *Poa pratensis* and *Taraxacum officinale*, on treeless south facing slopes in Elk Island National Park as a result of long-term overgrazing by bison.

In contrast to the gradient of disturbance to which plant species of different quadrat groups seem to responde, similar gradients were not easily revealed by the examination of mean group values for organic carbon, environmental variables, such as total clay, sand, mineral nitrogen, soil sodicity, and solar radiation (Figure 2-27d-i), and two spatial variables, longitude and latitude (Figure 2-27j, k). Direct gradient analyses used in this

study "disentangled" the complex relationships between these variables and allowed further interpretation of habitat characteristics that influence plant species composition at small scale.

Ordination of species and quadrats in multidimensional space defined by large- and small-scale environmental factors and disturbances

The first ordination axes of CCA-1 clearly separated undisturbed and lightly grazed quadrats dominated by *Festuca hallii* (quadrat Group A in Figure 2-8) from the rest of the quadrats (Figures 2-9 to 2-26). Because fallen and standing litter, organic carbon, and negatively correlated exposed mineral soil were the most important variables defining this axis (Table 2-5), the analysis clearly shows that disturbance is the main factor explaining variations in small-scale species composition in remnant grasslands. However, it is also clear that most of the explanation has been obtained from the variability in the abundance of a single species (*Festuca hallii*) in response to the disturbance. Species/environmental biplot of indicator, frequent, and common species for quadrat groups revealed an isolated position of *Festuca hallii* on the positive end of the axis that represented a low disturbance level, while the rest of the species crowded at the opposite end. Similarly, ordination showed that explained percent variability per species was significantly higher (63.41 %) for *Festuca hallii* than for the other species (Table 2-9). In addition, plant species that are often found on disturbed areas, including the majority of exotic species, were clearly positioned near the negative end of the first axis, which was characterized by higher disturbance (Figure 2-6).

However, examination of the second axis was required to explain more clearly the separation of the other quadrat groups (B-S) and to relate quadrat groups to the observed gradients defined by the means of the disturbance variables (fallen and standing litter, and exposed mineral soil). The second axis revealed a complex relationship between disturbance, environmental, and spatial variables in determining the plant species composition in quadrat groups. Four environmental (nitrogen, clay, sand, and solar radiation) and two spatial (latitude and longitude) variables that were important in defining the second axis of CCA-1 (Table 2-5) revealed a complex moisture gradient

(orthogonal to the gradient of disturbance) to which plant species in remnant grasslands of the aspen parkland respond. The two spatial variables, latitude and longitude, deserve special attention not only because both of them were highly correlated with the second axis (Table 2-5), but also because of their complex relation to the small-scale plant species composition in grasslands of the aspen parkland.

Firstly, the increase of latitude toward the positive end of the second axis, and that of longitude toward the opposite (negative) end, coincides with the expected climatically driven moisture gradient, with an increase of moisture from southeast toward the northwest of the aspen parkland. Thus, two spatial variables adequately represented moisture gradient at the large scale. On the species/environmental biplot from CCA-1, drought-tolerant species were clearly arranged near the negative end of the axis coinciding with a southeastern geographical position (Figure 2-3), while species that require ample moisture conditions for growth occupied the opposite (positive) end of the axis, coinciding with a northwestern geographical position (Figure 2-4).

Secondly, there was an interaction between the previously described moisture/spatial gradient and some of the soil characteristics in the remnants studied. Soils from remnants in two southern regions, Wainwright and Rumsey, belong to the Dark Brown Soil group that generally develops under vegetation exposed to a prolonged moisture deficiency (Toogood and Cairns 1978), but can also result from disturbances, such as grazing, that remove standing litter (Dormaar and Willms 1998). In contrast, more northern remnants at Kinsella and especially in Elk Island National Park regions developed on Black soils (the best agricultural soils), indicating relatively good moisture conditions throughout the growing season (Table 1-2, Figure 1-2, Chapter 1). The fact that Black soils of the aspen parkland are generally richer in mineral nitrogen than Dark Brown soils (Mitchell and Moss 1948) partially explains the positive correlation between mineral nitrogen and latitude.

Similarly, negative correlations between clay and silt variables on one hand and the sand variable on the other, indicate a gradient in soil texture characteristics, suggesting the

increase of the proportion of finer particles relative to the coarse ones from the southeast toward the northwest of the aspen parkland. This may be partially a result of higher organic matter in the Black soils of the northern areas, but southeastern location with sandy soils from one remnant in the Wainwright area (Table 1-2, Chapter1) certainly influenced the strength of the gradient. Although 30 quadrats were sampled on sandy soils from the northwest region of the aspen parkland (Elk Island National Park), they apparently did not affect the gradient of soil texture. Instead of being located near the negative end of the second axis with other indicators of dry sandy conditions, the majority of plant species collected from sands in the Elk Island National Park, as well as quadrats in which they were found, were arranged near the positive end of that axis (quadrat Group O, Figure 2-22). There are two explanations of this phenomenon. Firstly, the moisture index associated with Elk Island National Park has a much higher value then the values for areas in the southeastern part of the aspen parkland (Figure 1-2, Chapter 1). The Elk Island National Park is also heavily forested and has numerous wetlands. Thus, despite the rapid drainage that generally characterizes pockets of sandy soils (Crown 1977), a number of species that require ample moisture for growth were found there. Species, such as *Oryzopsis pungens* (Torr.) A. S. Hitchc. *Elymus canadensis* L., *Solidago spathulata, Corylus cornuta* Marsh, *Agropyron trachycaulum* var. *unilaterale*, and *Campanula rotundifolia* (see Figures 2-2, 2-3, 2-4), probably owe their presence on these sandy soils to the ample moisture that overrides the generally dry characteristics of coarse soil texture. Similarly, exotic species, such as *Trifolium repens*, *T. hybridum* L., and *Poa pratensis,* which contributed to the position of quadrats near the positive end of the second axis, probably owe their high abundance in these sandy soils to relatively good moisture conditions, and to the fact that they have been seeded in the past in different areas of the park from which they could be easily spread by park wildlife, especially bison (Achuff 1990).

Finally, latitude and longitude also represented a pure spatial gradient that determined the position of some environmental variables. Positive correlations between increased soil sodicity and latitude (Table 2-5) partially reflected the geographical distribution of Solonetzic soils within the aspen parkland of Alberta, mostly occupying central and

northwestern position within the parkland (Table 1-2, Chapter 1). These soils result from interaction between bedrock material and topography rather than climatic conditions. On species/environmental biplot, plant species that often indicate Solonetzic soils were placed near the positive end of the second axes, defined partly by increasing soil sodicity (Figure 2-5). Similarly, some of the positive correlation between solar radiation and longitude may have resulted from undersampling of south and southeast-facing slopes in the northwestern portion of the aspen parkland as a result of prevailing undulating terrain within the Elk Island National Park region (Table 1-2, Chapter 1). Finally, "clustering" of the quadrats from the same region and their clear spatial orientation within each quadrat group plotted on species/environment biplot (Figures 2-8 to 2-26) suggests that differences in propagule availability between the regions resulted from long-term separation of remnants by broken land.

In addition to the previously explained spatially structured components of small-scale environmental variables, solar radiation, sand, clay, nitrogen, and sodicity influenced plant species composition independently from the spatial position of the remnants. Mean values for the spatial positions of quadrat groups with high solar radiation and their large standard deviations indicated that numerous south and southeast-facing slopes accounted for the existence of drought-resistant species independently from general moisture conditions (geographical position) (Figures 2-27i, j, k). This agrees with Ayyad and Dix (1964) who found strong relationships between plant growth and slope and exposure in relatively undisturbed grasslands near Saskatoon, Saskatchewan. They also found that drought-tolerant species, such as *Bouteloua gracilis*, *Phlox hoodii* Richards, *Selaginella densa*, *Muhlenbergia cuspidata* (Torr.) Rydb., and *Stipa comata*, were associated with warm south or southeastern exposures. However, the strong association of *Festuca hallii* with moist, northern exposures reported by Ayyad and Dix (1964) disagrees with results of this study. The present study suggests the displacement of *F. hallii* from warmer sites only after disturbances, such as grazing. Ayyad and Dix (1964) indicated that only sites that "appeared to be free from recent grazing" were considered in their study. However, their indication of extremely high densities of *Selaginella densa* and *Flox hoodii* may suggest possibly more intense historical grazing on the Saskatchewan study sites, as it

was already speculated by Coupland and Brayshaw (1953). *Selaginella densa* was abundant only in moderately to heavily grazed areas in my study (quadrat group F). In the present study this species was of little importance in ungrazed or lightly grazed areas of the aspen parkland, and did not have significant cover values under rotational grazing at light to moderate intensities in the mixed-grass prairie of Alberta (Dormaar 1997).

Similarly, means of the spatial positions of the quadrat groups with high values of other environmental variables indicate that changes in mineral nitrogen, clay, and sodicity may have resulted from soil disturbances independently form the spatial gradient. Nitrogen could be increased as a result of windblown fertilizer from adjacent farmlands (Hobbs 1989), the invasion of nitrogen fixing species, such as *Trifolium* spp. (Mooney and Drake 1989), the activity of burrowing animals (Guo 1996, Grant et al. 1980), or from grazing regimes (Hobbs 1996). The increase in sodicity and the proportion of clay may have resulted from bringing the sodic B horizon to the surface, either by soil mixing or by the removal of the A horizon.

Partitioning of the explained variation in the species data set revealed that ca. 60% of the variation has been accounted for by non-spatial small-scale environmental variables and small-scale disturbances. The way in which small-scale environmental conditions, such as solar radiation, sand, nitrogen, and sodicity, could arise independently from spatial variables was previously explained. However, a significant positive correlation of exposed mineral soil with the positive end of the second axis may suggest a sampling bias towards more heavily disturbed quadrats being sampled in the northwestern region of the aspen parkland. Data on the distribution of disturbance types among the remnants clearly show that, although not identical, numbers of undisturbed or lightly disturbed quadrats and those with heavy disturbances were almost equally distributed among the regions (the proportion of more disturbed quadrats is actually slightly higher in the southeastern area) (Table 2-10). Moreover, examination of Table 2-3 indicates that quadrats associated with drier conditions (sandy soils, higher solar radiation, or southeastern position in the aspen parkland) have a significantly higher cover of lichen species compared to quadrats from moister areas, which partially explains the lower

percentage of exposed mineral soil in quadrats from drier areas. Around 12% of the explained variation has been accounted for by spatially-structured small-scale environmental variables (not pertaining to the disturbances). This would include interactions between regional moisture conditions with soil texture, nitrogen, and sodicity arising from the spatial position in the aspen parkland. Finally, ca. 28% of the explained variation has been accounted for by spatial variables alone, which most likely represents different propagule availability because of spatial separation of studied remnants.

Relative importance of large- and small-scale environmental factors, and disturbances for exotic plant species invasion

Examination of species/environment biplots (Figures 2-2 to 2-7) shows that the optima (realized niches) of the majority of exotic species fall in disturbed moist habitats. Native species do not show a clear preference along the moisture gradient but rather show a group specialization for specific environmental conditions. The preference of exotic species toward moister environments agrees with studies from other North American regions. For example, Forcella and Harvey (1983) found a decrease of exotic species abundance in very warm *Bouteloua-Stipa* grasslands in Montana. Numerous studies summarized by Mooney and Drake (1986) also suggested a negative response of exotic species to stressful conditions, such as drought. Exotic species in my study responded negatively to a lack of available moisture as a result of dry climatic conditions, coarse soil texture, or high solar radiation on south and southeast facing slopes.

The results of this study suggest that both preadaptation to anthropogenic disturbances and to ample moisture conditions similar to agricultural lands in the countries of origin play a role in the successful invasion of exotic species into fescue grasslands. A similar conclusion has been reached by Kanehiro and Mueller-Dombois (1995), who investigated the biological invasion of exotic species on an oceanic island mountain and found that a combination of climatic pre-adaptations of the exotic species and their historical evolvement with anthropogenic disturbances greatly influenced their distribution along an elevation gradient. However, the importance of the moisture gradient in the present study appears only after a disturbance. As predicted by Johnstone (1986), exotic species

need a "temporary window" or pre-empted space to become established, and their successful growth and reproduction further depend on moisture conditions. Rejmánek (1989) reviewed numerous studies in order to investigate the exotic species invasion along a moisture gradient and suggested that mesic habitat conditions are more prone to invasion than xeric or hydric ones. In addition, larger propagules and a reduced dispersal capacity characterize species inhabiting xeric areas due to the necessity of forming deep roots in dry soil (Platt 1975). Exotic ruderal species often have light seeds in order to enhance wind dispersal, therefore this allocation of resources toward dispersal may hinder their successful establishment under dry conditions (Grime et al. 1988).

Higher values for moisture indices (P-PEP) in the northwest region of Alberta coincide with higher soil fertility which may further enhance exotic species invasion. As experimental studies from remnant native vegetation near Kellerberrin, Australia, have found, a combination of both disturbance and good nutrient conditions are required for the successful establishment of exotic species (Hobbs 1989). Therefore, disturbances that result in simultaneous increase of several resources, such as light and nutrients, will more likely lead to the successful invasion of exotic species than ones that will affect only one of the resources (light or nutrients). Exotic species are known to respond better than native ones to the addition of nutrients. In the present study, increased soil mineral nitrogen in combination with disturbance and ample moisture conditions resulted in replacement of *Festuca hallii* by the exotic, rhizomatous, drought sensitive species, *Poa pratensis.* When grown without competition, *Poa pratensis* growth increased significantly after nitrogen fertilization under experimental conditions, while the native species *Schizachyrium scoparium* (Michx.) Nees, was not affected by additional nitrogen availability (Wilson and Tilman 1991).

Conversely, native species show a group specialization toward specific environmental conditions, therefore representing preadaptations to both climatic and local environmental conditions, including small-scale disturbances. *Festuca hallii* occupies undisturbed to moderately grazed areas characterized by diverse soil conditions. Numerous drought tolerant species (e.g., *Bouteloua gracillis*, *Selaginella densa*, *Stipa comata*) occupy

disturbed drier areas, facultative halophytes (e.g., *Grindelia squarrosa*, *Distichlis stricta* (Torr.) Rydb., *Agropyron smithii*) occur in disturbed areas with increased sodicity, and fugitive species thrive on either dry or mesic heavily disturbed areas (e.g., *Lepidium densiflorum*, *Solanum triflorum* Nutt., *Spheralcea coccinea* St. Hil.). Still, the majority of native species (e.g., *Androsace septentionalis* L., *Antennaria* spp., *Thermopsis rhombifolia* (Nutt.) Richards.) are characterized by a wide distribution along different gradients resulting in a high unexplained variability within the species data matrix. High preadaptations of the majority of native species to disturbances may be related to co-evolution with bison. Extensive documentations indicate the historical presence of numerous bison herds in the aspen parkland (e.g., Morgan 1980, Fidler 1990, Campbell 1994). Allen (1967) described local disturbances caused by these big, hoofed animals in localized areas, and pointed out the temporary "healing" of the disturbed ground through stages of annual grasses and forbs toward pre-disturbance conditions.

Small-scale vascular plant species composition in the fescue grasslands in relation to the "centrifugal organization model"

Results of this study suggest that the assembly of plant species in fescue prairie grasslands in the aspen parkland may follow the "centrifugal organization model". This process-oriented model (Keddy 1990a, b) describes the pattern of species composition along environmental gradients and incorporates underlying mechanisms. The model was derived from patterns (centrifugal organization) and processes (core habitats and competitive hierarchies) observed in temperate zone wetlands and forests (Keddy 1990b). The distribution pattern of species along a biomass gradient shows similar plant composition at one end (productive and/or undisturbed) but highly variable at the other end (the end with low productivity and/or high disturbances). This model also predicts a decrease in the species pool and the number of life forms with increasing biomass. The highest biomass should occur in the core habitat that supports only one large rhizomatous canopy-forming species. This species is usually at the top of the competitive hierarchy, which explains the absence of species with lower competitive abilities in the core habitat. As fertility decreases and/or disturbance increases to the "periphery" of the model, different combinations of environmental constraints will result in variable species

compositions, characterized by species lower in the competitive hierarchy (Keddy 1990b). While the core habitat in the centrifugal organization model may be a fundamental niches for species from both ends of the tested gradient, the environments at the periphery of the model probably represent realized niches for inhabiting species (Keddy 1990a). Finally, this model proposed a control for the species composition along any specific gradient by one-sided competition. Upon the removal of a strong competitor, less competitive neighbors can move toward the "core" habitat, but species from the top of the competitive hierarchy can not move toward sites at the periphery (Keddy 1991).

In this study, undisturbed areas of fescue grassland in the aspen parkland of Alberta clearly represent a "core" habitat dominated by a single species, *Festuca hallii*. It is not until a disturbance lowers the competitive abilities of that relatively tall, rhizomatous perennial plant, that other species has the opportunity to invade "core" fescue stands. Once disturbance occurrs, species composition is constrained by the disturbance intensity and environmental gradients of moisture, sodicity, and mineral nitrogen. This results in a high number of quadrat groups (18) radiating toward the "periphery" of the model (Figure 2-28).

As predicted by the centrifugal organization model, after the partial or total removal of the competitor (*Festuca hallii*), species from the periphery (indicators of disturbance, sodicity, and drought conditions) invaded habitats that were previously occupied by the competitor. Although the strongest competitor under undisturbed conditions, *Festuca hallii* is not able to "move" toward the peripheral (disturbed) habitats. However, the ability of fescue to persist as a component of the species assemblage under disturbed conditions varies along the moisture gradient, such that dry environmental conditions enhance its persistence, while moist conditions, combined with high disturbance, caused its replacement by ruderal species (including exotics).

To conclude, highly predictable species assemblage in undisturbed sites with high biomass become replaced with numerous, less predictable species assemblage in relation to changes in small-scale environmental conditions and underlying general climatic

conditions. Ordination indicated that disturbed mesic areas are more affected by same kind of disturbances (have higher percent of exposed mineral soil) then drier ones, resulting in a pool of species that prefer ample moisture conditions and higher disturbance levels (numerous annuals, including exotics). However, what combination of these species will be sampled at the small-scale at any given moment will probably be highly unpredictable, because of differences in sodicity, fertility, the small quadrat size, and differences in successional stages. The same comment applies to the drier sites, where numerous combinations of drought-resistant species (but rarely exotics) from the pool may be drawn at any given point of time. Similarly, Ayyad and Dix (1964), who investigated plant species distribution in relation to aspect and slope in the prairie grasslands near Saskatoon, Saskatchewan, suggested that the extremely gradual variation of the species composition along the moisture gradient (aspect/slope) would make the establishment of any vegetation unit highly subjective. Chance plays a significant role in determining the small-scale species composition in grassland communities (Glenn and Collins 1993, Collins and Glenn 1991).

Fescue grasslands from this study differed from wetland and forest communities discussed with respect to the centrifugal organization model (Keddy 1990a,b, Gaudet and Keddy 1995) in that the core habitat did not represent the most fertile one. The only macronutrient measured in this study, mineral nitrogen, not only showed an average value for the undisturbed "core" quadrat group characterized by *Festuca hallii* (Figure 2-27f), but, as previously discussed, mineral nitrogen also had the highest values in some disturbed, mesic habitats. This suggests that in ecosystems, such as fescue grasslands, the species assembly along a fertility gradient may not follow the centrifugal organization model the way that wetlands and forests do. The levels of mineral nitrogen are normally low in native fescue pastures because of their rapid utilization by the grassland vegetation (Dormaar et al. 1990). Disturbances, such as cattle grazing (Dormaar et al. 1990) and animal burrowing (Guo 1996, Grant et al. 1980), result in increased levels of nitrogen, which, combined with the space opening mediated by disturbances, may result in the establishment of exotic species, such as *Poa pratensis*. Indeed, in this study, quadrats with a high abundance of *P. pratensis* were also characterized by heavy grazing and the

highest mean mineral nitrogen content (quadrat group J in Figure 2-27f). However, this study was not intended to explore the species composition along a fertility gradient in fescue grasslands. An experimental study or a more careful sampling design that includes a larger number of soil nutrients, a wider range of fertility, and more specific timing of measurements (earlier in the growing season, or more frequently during the season) may be needed to explore this relationship.

Scientific Contribution

This is the first comprehensive study to investigate plant species composition in relation to the large- and small-scale environmental conditions and small-scale disturbances in numerous grasslands across the aspen parkland. Sampling under the fences and inside the long-term enclosures provided areas that remained protected from grazing or were infrequently grazed but not trampled for more then twenty years. This method allowed for the identification of the small-scale disturbances as the most important factor in explaining differences between undisturbed areas of grasslands dominated almost exclusively by *Festuca hallii* and areas with higher species diversity where disturbance level and underlying environmental conditions, such as moisture, soil sodicity, soil nitrogen level, and stochastic events determine the species composition. This study is the first to demonstrate the generally accepted positive relationship of exotic species with disturbance and moisture gradients in native grasslands. Finally, this study showed that the "centrifugal organization model", previously discussed only for forest and wetland communities, may be applicable for a grassland community, as well.

Conclusions

Disturbance acts as a major factor influencing small-scale plant species composition in remnant fescue grasslands in the aspen parkland of Alberta. A "climax" species, *Festuca hallii*, dominates undisturbed or lightly disturbed areas to the exclusion of most other vascular plant species. Once disturbance takes place, the species composition is constrained by the magnitude of the disturbance and environmental conditions, such as moisture, soil sodicity, and soil mineral nitrogen. Different small-scale disturbances in combination with different large- and small-scale environmental conditions result in the

diversity of species assemblies at the small scale. Different combinations of drought-resistant species invade fescue grasslands in drier areas, halophytes invade soils with increased sodicity, and ruderals become important component of mesic areas. Exotic species preferably invade disturbed, mesic areas, thereby clearly expressing co-evolution with the anthropogenic (mainly agricultural) disturbances in countries of their origin. Finally, the small-scale composition of vascular plant species in the fescue grasslands seems to be consistent with the "Centrifugal organization model".

Table 2-1. Summary of the thirteen environmental variables used in CCA analyses.

Variable	Abbreviation	Explanation
Fallen litter	FALLIT	Depth of fallen dead plant material detached from the soil (cm)
Standing litter	STALIT	Height of dead standing plant material attached to the soil (cm)
Exposed mineral soil	EXMISO	Cover of exposed mineral soil (%)
Organic carbon	OC	Soil organic carbon (%)
Mineral Nitrogen	MINN	Total mineral nitrogen in the soil (NH_4-N, NO_3-N) (ppm)
Sodium Adsorption Ratio	SAR	Relative activity of sodium ions in exchange reaction with soil
Electrical conductivity	EC	Conductivity of saturation extract from soil (dS/m *)
Solar radiation	SOLRAD	Mean annual solar radiation received by the quadrate (KJ/cm^2 **)
Total clay	CLAY	Proportion of course particles in soil (0.2-2mm) (%)
Total silt	SILT	Proportion of medium particles in soil (0.02-0.2mm) (%)
Total sand	SAND	Proportion of fine particles in soil (0.002-0.02mm) (%)
Latitude	UTM-E	7 digit number indicating latitudinal geographical position
Longitude	UTM-N	6 digit number indicating longitudinal geographical position

* dS/m = deciSiemens per meter

** KJ/cm^2 = Kilojoules per square centimeter

Table 2-2. Matrix of vascular plant species and quadrat groups. Percentages are mean percent cover for the indicator species (occur in every quadrat), frequent species (occur in at least 70% of quadrats), and species occurring in at least half of the quadrates but not being frequent. Bold mean values are given to the indicator species and mean values for frequent species are underlined. Bold species name indicates exotic species (*Poa pratensis* is underlined because of its questionable origin). The full scientific names for vascular plant species with associated six-letter codes are listed in Appendix 1.

Species code	Quadrat Groups																		
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
FESHAL	73.8	12.9	10.1	6.9	19.3	5.3	3.1	3.0	-	-		-	-	-	-	-	-	-	-
STICUR	4.6	19.8	7.0	-	-	5.4	4.7	8.0	2.4	-	-	1.8	3.0	-	-	2.1	-	7.3	-
ANEPAT	3.2	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ACHMIL	2.3	2.6	3.1	3.0	-	-	-	1.8	-	4.4	3.6	-	3.5	-	5.2	-	-	-	-
AGRUNI	-	3.6	2.1	-	-	-	-	-	-	-	-	1.8	-	-	2.7	-	-	3.0	-
SOLMIS	-	3.1	-	-	-	-	-	-	-	-	-	1.4	3.3	-	-	-	-	-	-
ARTFRI	-	4.2	-	-	2.3	4.4	3.8	1.9	19.3	-	-	2.8	-	3.6	-	2.2	2.4	-	-
CAROBT	-	4.3	4.0	-	-	-	-	-	-	-	-	-	10.7	-	-	-	-	-	-
KOEMAC	-	2.1	-	-	-	2.6	3.4	2.9	-	-	-	-	1.8	-	-	-	-	-	-
ROSSPP	-	1.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CERARV	-	-	2.0	-	-	-	-	-	-	-	-	-	2.2	-	-	-	-	-	-
AGRSCA	-	-	6.2	3.4	-	-	-	-	-	-	-	1.0	3.0	2.5	-	-	-	-	-
ANTSPP	-	-	18.6	-	-	-	6.1	5.6	-	-	-	-	-	-	-	-	-	-	-
ASTERI	-	-	1.9	-	-	-	-	-	-	4.8	-	-	3.7	-	-	-	-	-	-
DANCAL	-	-	15.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VICAME	-	-	-	1.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
JUNHOR	-	-	-	-	74.0		-	-	-	-	-	-	-	-	-	-	-	-	-
SELDEN	-	-	-	-	-	59.7	-	-	-	-	-	-	-	-	-	-	-	-	-
CARPEN	-	-	-	-	-	11.2	9.1	-	-	-	-	3.2	-	-	-	-	-	-	-
BOUGRA	-	-	-	-	-	-	5.3	8.5	-	-	-	1.8	-	7.3	-	-	-	4.0	-
SYMOCC	-	-	-	-	-	-	-	33.1	-	-	-	-	-	-	-	-	-	-	-

POTCON	-	-	-	-	-	-	-	1.8	-	-	-	1.6	-	-	-	-	-	-	-
TAROFF	-	-	-	1.6	-	-	-	-	-	3.6	6.9	-	2.0	-	-	-	-	-	3.1
AXYAMA	-	-	-	-	-	-	-	-	2.1	-	-	-	-	-	-	-	-	-	-
AGRSMI	-	-	-	-	-	-	-	-	-	4.4	-	-	3.0	21.0	-	-	-	7.8	-
POAPRA	-	-	-	-	-	-	-	-	-	49.8	14.5	8.0	-	-	2.8	-	-	-	-
TRIREP	-	-	-	-	-	-	-	-	-	-	23.3	-	-	-	4.9	-	-	-	-
PSOARG	-	-	-	-	-	-	-	-	-	-	-	3.2	-	-	-	-	-	-	-
STIVIR	-	-	-	-	-	-	-	-	-	-	-	8.1	-	-	-	-	-	-	-
GRISQU	-	-	-	-	-	-	-	-	-	-	-	1.5	7.8	2.4	-	-	-	-	-
MUHRIC	-	-	-	-	-	-	-	-	-	-	-	-	10.3	-	-	-	-	-	-
CARSTE	-	-	-	-	-	-	-	-	-	-	-	-	-	12.0	-	-	-	-	-
CARSIC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.3	-	-	-	-
ARTCAM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9.2	-	-	-	-
CAMROT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.4	-	-	-	-
RUMACE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.4	-	-	-	-
SOLSPA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.4	-	-	-	-
CHEALB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.6	-	1.0	-
MONNUT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.1	-	-	-
POLARE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.2	0.7	-	4.0
BROINE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.8	-	-
MELALB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.8	-	-
LEPDEN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28.5	-
PUCNUT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.4
AGRREP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19.0

Table 2-3. Matrix of non-vascular plant species and quadrat groups. Percentages are mean percent cover for the species that occur in at least 50% of quadrats (bold) and species occurring in less then a half of the quadrats. The full scientific names for non-vascular plant species with associated six-letter codes are listed in Appendix 1.

Species	A	B	C	D	E	F	G	H	I
Mosses									
POLJUN	15.5	14.4	**27.8**	17.0	-	3.0	-	1	-
BRASPP	**29.6**	34.0	11.3	**10.9**	-	5.0	-	0.1	-
CERPUR	7.4	20.0	13.2	5.0	-	3.0	3.0	-	4.3
TORRUR	13.3	4.0	41.67	35.0	**21.3**	-	2.0	-	30.0
ABIABI	24.4	34.0	10.2	3.7	**20.3**	-	-	-	3.0
BRYSPP	1.0	-	-	-	-	-	-	-	-
AMBSPP	3.6	5.0	0.8	5.0	-	-	-	-	-
BARSPP	1.0	0.1	-	-	-	-	-	-	-
EURPUL	55.4	30.0	-	-	-	-	-	-	-
PLESCH	20.0	-	-	-	-	-	-	-	
DREUNC	0.1	-	-	-	-	-	-	-	-
HYLSPL	5.0	-	-	-	-	-	-	-	-
BRYARG	-	0.1	-	-	-	-	-	-	-
BRYCAE	1.0	-	-	-	-	-	0.1	1.0	0.1
CAMSPP	8.7	1.0	1.0	-	-	-	-	-	-
BRASAL	40.6	-	-	5.5	-	-	-	-	-
HAPSPP	25.1	-	-	-	-	-	-	-	-
Lichens									
CLAMUL	25.1	26.0	**17.5**	20.0	-	34.0	42.5	50.0	2.0
CLAPYX	**24.8**	**32.8**	24.2	5.0	**6.3**	**25.1**	**35.6**	**24.0**	4.8
CLAMIT	32.8	12.4	24.6	1.0	12.5	29.4	20.3	-	2.0
CLACOR	12.5	0.1	1.0	-	-	-	-	-	-
PELRUF	5.0	2.5	0.1	4.0	2.0	1.5	0.1	-	-
CLAPOC	-	-	-	-	-	-	-	-	-
CLAFIM	9.4	30.1	-	10.0	-	-	-	-	-
CLAGRA	-	0.6	0.7	-	-	-	-	-	-
CLACAR	-	-	-	-	-	-	-	-	-
PELDID	0.1	-	0.1	-	-	-	-	-	-
CLASCA	14.3	0.1	-	-	-	-	-	-	-
PELLEP	-	-	0.1	-	-	-	1.0	-	-
CLAMAC	0.4	-	-	-	-	-	-	-	-
PHYMUS	-	0.1	0.1	-	-	-	-	-	0.1
XANCHL	-	-	-	-	-	5.5	-	-	1.0
CLASQU	4.3	0.1	0.1	-	-	-	-	-	-
CLACHL	0.1	0.1	-	-	-	-	-	-	-
PARSUL	0.1	-	-	-	-	-	-	-	-
USNLAP	0.1-	-	-	-	-	-	-	-	-
PHYADS	0.1	-	-	-	-	-	-	-	-
EVEMES	0.1	-	-	-	-	-	-	-	-
CETACU	-	-	-	-	1.0	1.0	-	-	-
CETERI	-	-	-	-	6.0	1.7	8.0	-	-
CLACEN	-	-	-	-	-	-	-	-	-
CLAPHY	-	0.1	-	-	-	-	-	-	-
CLACON	-	-	-	-	-	-	-	-	-
CALSPP	-	-	-	-	-	-	-	-	0.1

Species	J	K	L	M	N	O	P	Q	R	S
Mosses										
POLJUN	1.0	2.0	-	32.3	35.0	3.4	-	-	-	-
BRASPP	5.9	5.5	-	10.8	-	3.5	45.0	-	-	-
CERPUR	0.7	1.0	-	1.0	20.0	4.1	-	-	-	-
TORRUR	50.0	2.0	-	53.7	26.8	-	-	6.0	-	1.0
ABIABI	20.0	23.4	-	1.0	-	1.0	5.0	-	-	-
BRYSPP	30.0	-	-	-	-	0.1	-	5.0	-	-
AMBSPP	5.0	10.0	-	1.0	-	-	-	-	-	-
BARSPP	0.1	-	2.0	-	-	-	-	-	-	-
EURPUL	1.0	-	-	-	-	-	-	-	-	-
PLESCH	-	-	-	-	-	-	-	-	-	-
DREUNC	-	-	-	-	-	-	-	-	-	-
HYLSPL	-	-	-	-	-	-	-	-	-	-
BRYARG	-	-	-	-	-	-	-	-	-	-
BRYCAE	0.1	-	2.0	10.0	-	-	-	-	-	-
CAMSPP	8.7	2.0	-	-	-	-	-	-	-	-
BRASAL	-	-	-	-	-	30.0	-	1.0	-	-
HAPSPP	-	-	-	-	-	-	-	-	-	-
Lichens										
CLAMUL	-	1.0	-	21.0	-	-	-	-	-	-
CLAPYX	20.0	4.8	-	13.8	1.4	2.1	-	7.0	1.5	-
CLAMIT	-	-	-	2.3	-	1.4	-	-	-	-
CLACOR	-	-	-	-	-	-	-	-	-	-
PELRUF	-	20.0	-	2.0	-	1.8	-	2.0	-	-
CLAPOC	-	-	-	5.0	-	2.0	-	-	-	-
CLAFIM	-	-	-	-	-	3.0	-	-	-	-
CLAGRA	-	-	-	1.0	-	-	-	-	-	-
CLACAR	-	-	-	-	-	5.0	-	-	-	-
PELDID	0.1	-	-	40.0	-	0.7	-	-	-	-
CLASCA	-	-	-	-	-	-	-	-	-	-
PELLEP	0.1	-	-	-	-	-	-	-	-	-
CLAMAC	-	-	-	-	-	-	-	-	-	-
PHYMUS	-	-	-	-	-	-	-	0.1	-	-
XANCHL	-	-	-	-	-	-	1.0	-	-	-
CLASQU	-	-	-	-	-	-	-	-	-	-
CLACHL	0.1	-	-	-	-	-	-	-	-	-
PARSUL	-	-	-	-	-	-	-	-	-	-
USNLAP	-	-	-	-	-	-	-	-	-	-
PHYADS	-	-	-	-	-	-	-	-	-	-
EVEMES	-	-	-	-	-	-	-	-	-	-
CETACU	-	-	-	-	-	-	-	1.0	-	-
CETERI	-	-	-	-	-	0.1	-	1.1	-	-
CLACEN	0.1	-	-	-	-	-	-	-	-	-
CLAPHY	-	-	-	50.0	-	-	-	-	-	-
CLACON	-	-	-	-	-	0.6	-	-	-	-
CALSPP	-	-	-	-	-	-	-	-	-	-

Table 2-4. Summary of canonical correspondence analysis (CCA-1) of 484 quadrats from 11 remnant grasslands in the Aspen Parkland Ecoregion of Alberta.

Axis	1	2	3	4	Σ
Eigenvalue	0.39	0.29	0.14	0.12	
Species/environmental correlation	0.83	0.73	0.68	0.65	
Cumulative % variance of:					
species data explained	3.7	6.5	7.8	9.0	
species/environmental relation explained	31.3	54.5	65.4	75.0	
Unconstrained eigenvalues					10.386
Canonical eigenvalues					1.25

Table 2-5. Statistics for environmental variables (including spatial position) used in canonical correspondence analysis (CCA-1) of 484 quadrats from 11 remnant grasslands in the Aspen Parkland Ecoregion of Alberta. Absolute t-value > 1.96 was used to identify important canonical coefficients (ter Braak 1988). Asterisks indicate significance at $p < 0.05$. Absolute $\rho > 0.09$ was used to identify significant inter set correlation at $p < 0.05$. Bold values indicate variables with significant correlation and canonical coefficients. Variables are coded as follows: EXMISO-exposed mineral soil; FALLIT-fallen litter; STALIT-standing litter; OC-organic carbon; SOLRAD-solar radiation; MINN-mineral nitrogen; EC-electrical conductivity; SAR-Sodium Adsorption Ratio; CLAY-total clay; SAND-total sand; UTM-E-longitude; UTM-N-latitude.

	Inter set correlation		Canonical coefficient		t-value	
Variables	Axis1	Axis2	Axis1	Axis2	Axis1	Axis2
EXMISO	**-0.43***	**0.21***	-0.20*	0.34*	-5.32*	6.65*
FALLIT	**0.75***	-0.04	0.67*	-0.07	16.46*	-1.25
STELIT	**0.54***	-0.01	0.23*	0.06	6.05*	1.22
OC	**0.34***	0.18	0.21*	-0.06	4.08*	-0.81
SOLRAD	**-0.21***	**-0.25***	-0.13*	-0.22*	-3.79*	-4.67*
MINN	0.06*	**0.40***	-0.13*	0.19*	-3.32*	3.40*
EC	-0.15	0.33	-0.10	-0.01	-1.95	-0.22
SAR	-0.07	0.41	-0.04	0.16	-0.67	1.91
CLAY	0.08	**0.24***	0.27*	-0.20*	4.67*	-2.57*
SAND	**-0.19***	**-0.32***	0.17*	-0.35*	2.59*	-3.78*
UTM-E	-0.13	**-0.60***	-0.09	-0.55*	-2.16*	-9.95*
UTM-N	0.06*	**0.39***	0.11*	0.21*	2.88*	4.10*

Table 2-6. Summary of the canonical correspondence analysis (CCA-2) of 484 quadrats from 11 remnant grasslands in the Aspen Parkland Ecoregion of Alberta.

Axis	1	2	3	4	Σ
Eigenvalue	0.39	0.24	0.12	0.08	
Species/environmental correlation	0.82	0.71	0.66	0.52	
Cumulative % variance of:					
species data explained	3.7	6.1	7.2	8.0	
species/environmental relation explained	36.8	60.2	71.8	79.1	
Unconstrained eigenvalues					10.386
Canonical eigenvalues					1.045

Table 2-7. Statistics for environmental variables used in canonical correspondence analysis (CCA-2) of 484 quadrats from 11 remnant grasslands in the Aspen Parkland Eco-region of Alberta. Absolute t-value > 1.96 was used to identify important canonical coefficients (ter Braak 1988). Asterisks indicate significance at $p < 0.05$. Absolute $\rho > 0.09$ was used to identify significant inter set correlation at $p < 0.05$. Bold values indicate variables with significant correlation and canonical coefficients. Variables are coded as follows: EXMISO-exposed mineral soil; FALLIT-fallen litter; STALIT-standing litter; OC-organic carbon; SOLRAD-solar radiation; MINN-mineral nitrogen; EC-electrical conductivity; SAR - Sodium Adsorption Ratio; CLAY-total clay; SAND-total sand.

	Inter set correlation		Canonical coefficient		t-value	
Variables	Axis1	Axis2	Axis1	Axis2	Axis1	Axis2
EXMISO	**-0.44***	**0.19***	-0.21*	0.39*	-5.75*	7.23*
FALLIT	**0.75***	0.04	0.67*	0.01	16.23*	0.18
STELIT	**0.53***	0.05	0.23*	0.10	5.91*	1.74
OC	**0.32***	0.24	0.24*	0.06	4.49*	0.85
SOLRAD	**-0.19***	**-0.24***	-0.13*	-0.28*	-3.71*	-5.79*
MINN	0.03*	**0.43***	-0.12*	0.41*	-3.21*	7.51*
EC	**-0.18***	0.39	-0.12*	-0.04	-2.19*	-0.53
SAR	-0.08	**0.46***	0.01	0.48*	0.19	5.80*
CLAY	0.07*	0.32	0.31*	-0.01	5.31*	-0.15
SAND	**-0.17***	**-0.43***	0.22*	-0.35*	3.22*	-3.55*

Table 2-8. Partitioning of variation between non-spatial environmental and spatial variables.

Constraint in CCA	Sum of canonical variables	% variance
1. Environmental variables only	1.045	10.06
2. Geographical coordinates only	0.613	5.9
3. All variables minus geographycal variables	0.86	8.28
4. All variables minus environmental variables	0.428	4.12
Variance partitioning		
1. Non-spatial environmental (3 above)		8.28
2. Spatial not shared with environmental (4 above)		4.12
3. Spatialy structured environmental (1 - 3 above)		1.78
4. Unexplained variation (100% - (1 + 4 above)		85.82

* % variance is the total variation of the species matrix accounted for by each of four steps of the partitioning of the variation between spatial and non-spatial environmental components.

Table 2-9. Percent variance explained per vascular plant species, as obtained by CCA-1 and presented in Cfit table of Canoco.sol file. Only species with variance explained greater than 10% are presented. The full scientific names for vascular plant species with associated six-letter codes are listed in Appendix 1.

Species code	% Explained
ACHMIL	16.94
AGRSMI	15.19
AGRUNI	10.05
ANEPAR	11.20
ARTCAM	12.35
ARTFRI	10.47
ASTERI	10.28
BOUGRA	17.37
CAMROT	13.11
CAROBT	11.85
CARPEN	23.52
CARPRT	13.60
CARSIC	21.79
CERARV	15.16
CHEALB	14.16
CORCOR	10.30
DANCAL	17.60
ERIGLA	11.69
FESHAL	63.41
FESSAX	12.93
GALBOR	20.27
GRISQU	22.89
KOEMAC	15.29
LEPDEN	14.44
PENPRO	12.19
PHLHOO	10.72
POACAN	12.81
POAPRA	16.47
POLARE	11.63
POTCON	10.16
RUMACE	12.04
SALPET	14.60
SOLSPA	29.79
SELDEN	17.91
STICUR	19.51
TAROFF	16.41
THERHO	15.57
TRIREP	13.65
VIOADU	11.28

Table 2-10. Numerical distribution of different types of disturbances among 11 remnant grassland areas in four geographical regions.

Disturbance level	"Region"			
	Wainwright	Rumsey	Kinsella	Elk Island National Park
Undisturbed	3	6	22	4
Light grazing	13	12	2	25
Medium grazing	45	38	47	44
Old soil mixing	1	8	0	6
Heavy grazing	11	17	3	18
Soil trampling	20	11	23	11
Removal of up to 10 cm of soil	7	10	5	3
Removal of more than 50 cm of soil	8	0	7	6
Recent soil mixing	7	10	2	4
Removal of 10-30 cm of soil	8	6	8	8

Figure 2-1. Nineteen quadrat groups (A to S) derived by the unweighted arithmetical average clustering. Due to large number of quadrats included in clustering (479) only part of the dendrogram above the chosen cutline (Bray-Curtis dissimilarity coefficient = 0.725) is presented.

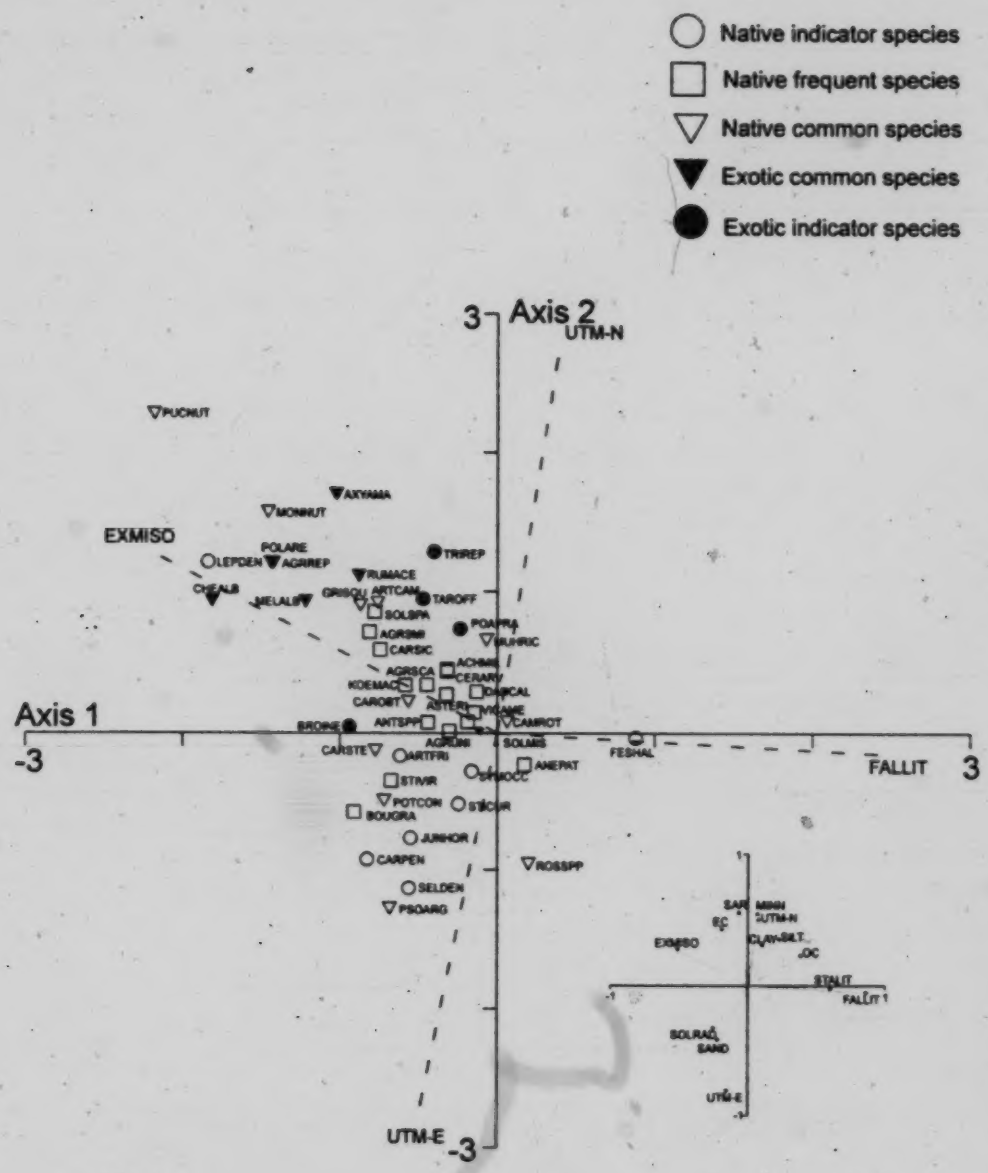

Figure 2-2. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays indicator species, frequent species (F>70%) and common species (F>50%) for 19 quadrat groups derived by UPGMA. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

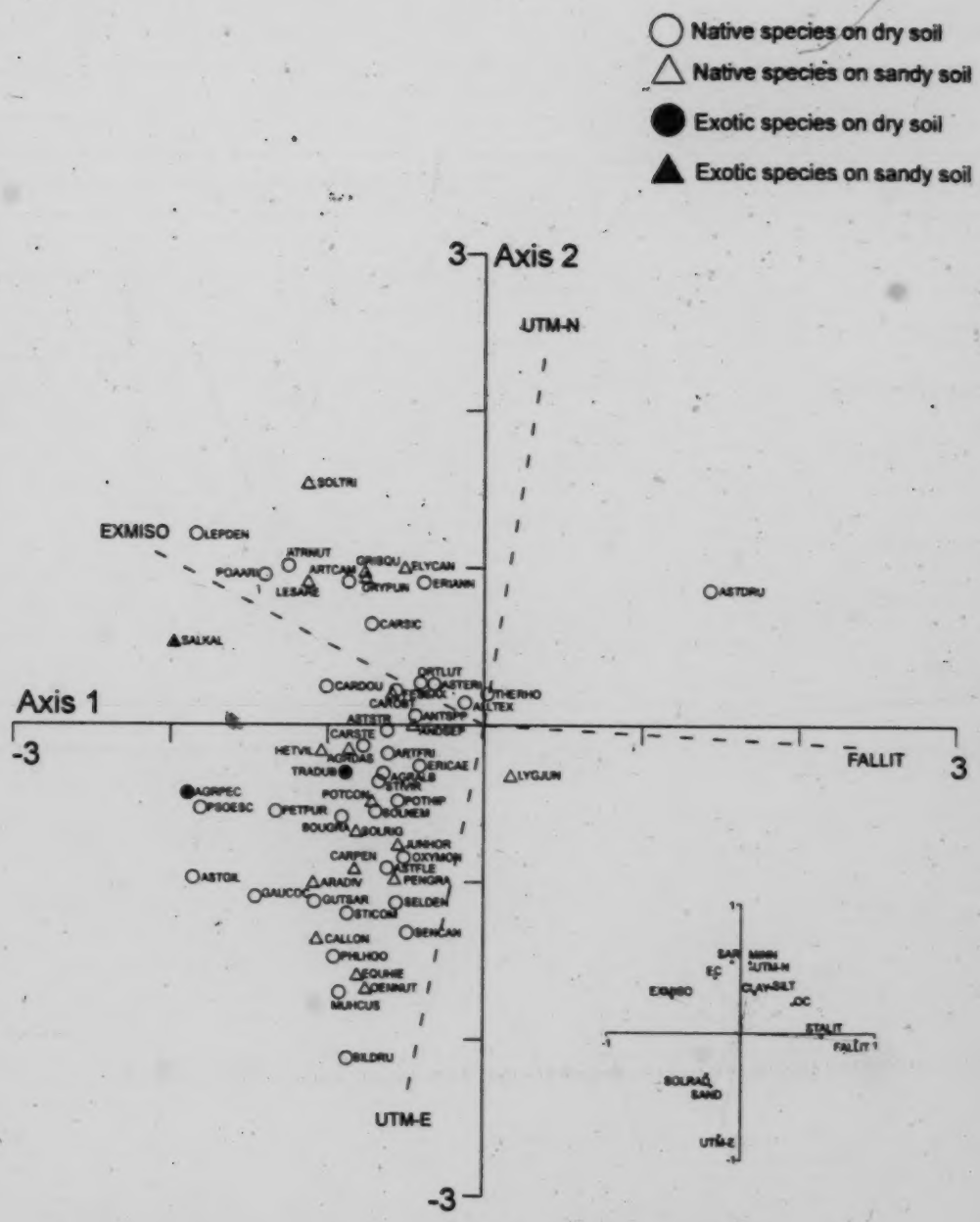

Figure 2-3. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays indicator species for dry or sandy soil conditions only. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

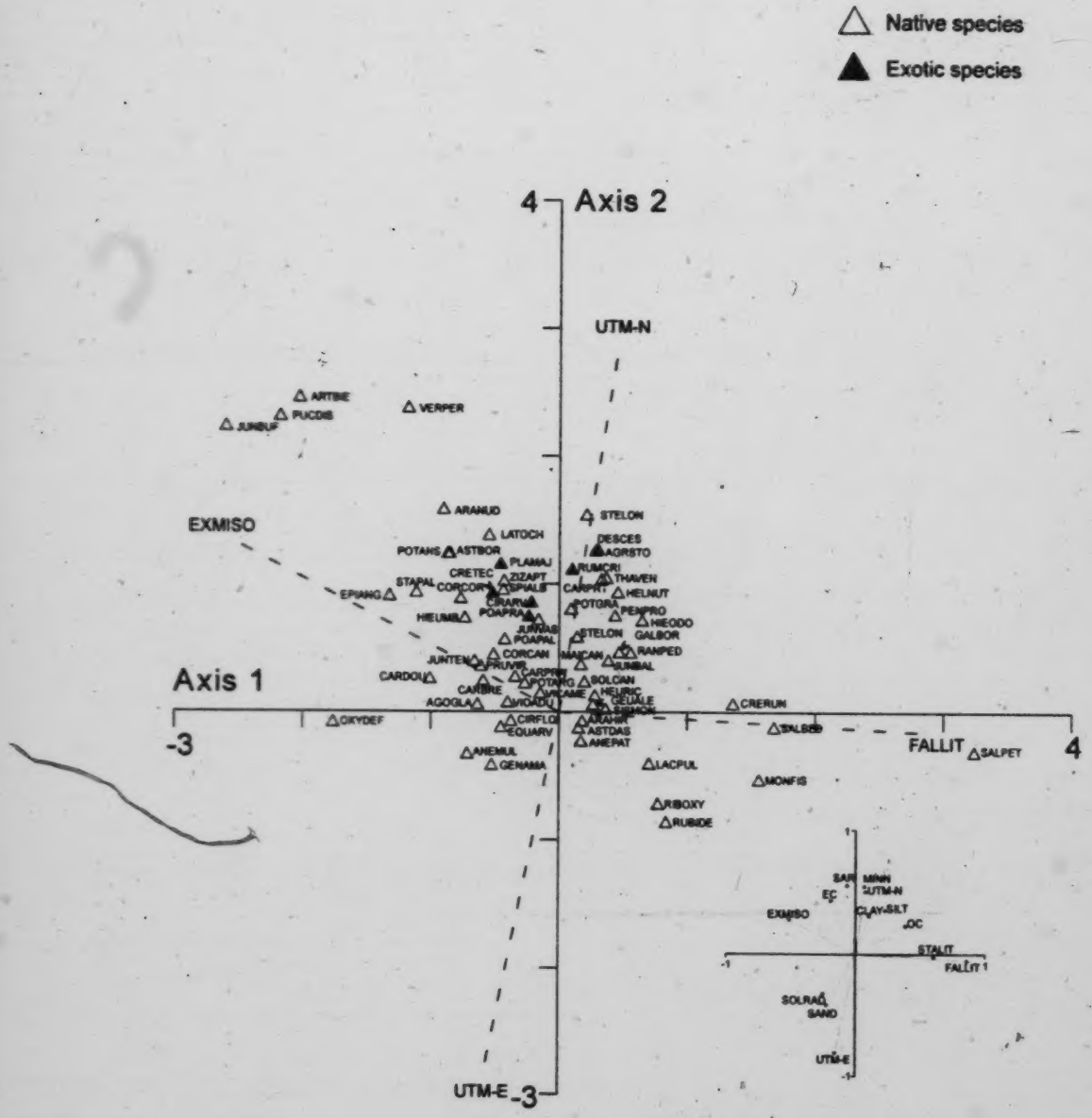

Figure 2-4. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays species that indicate moist to wet soil conditions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

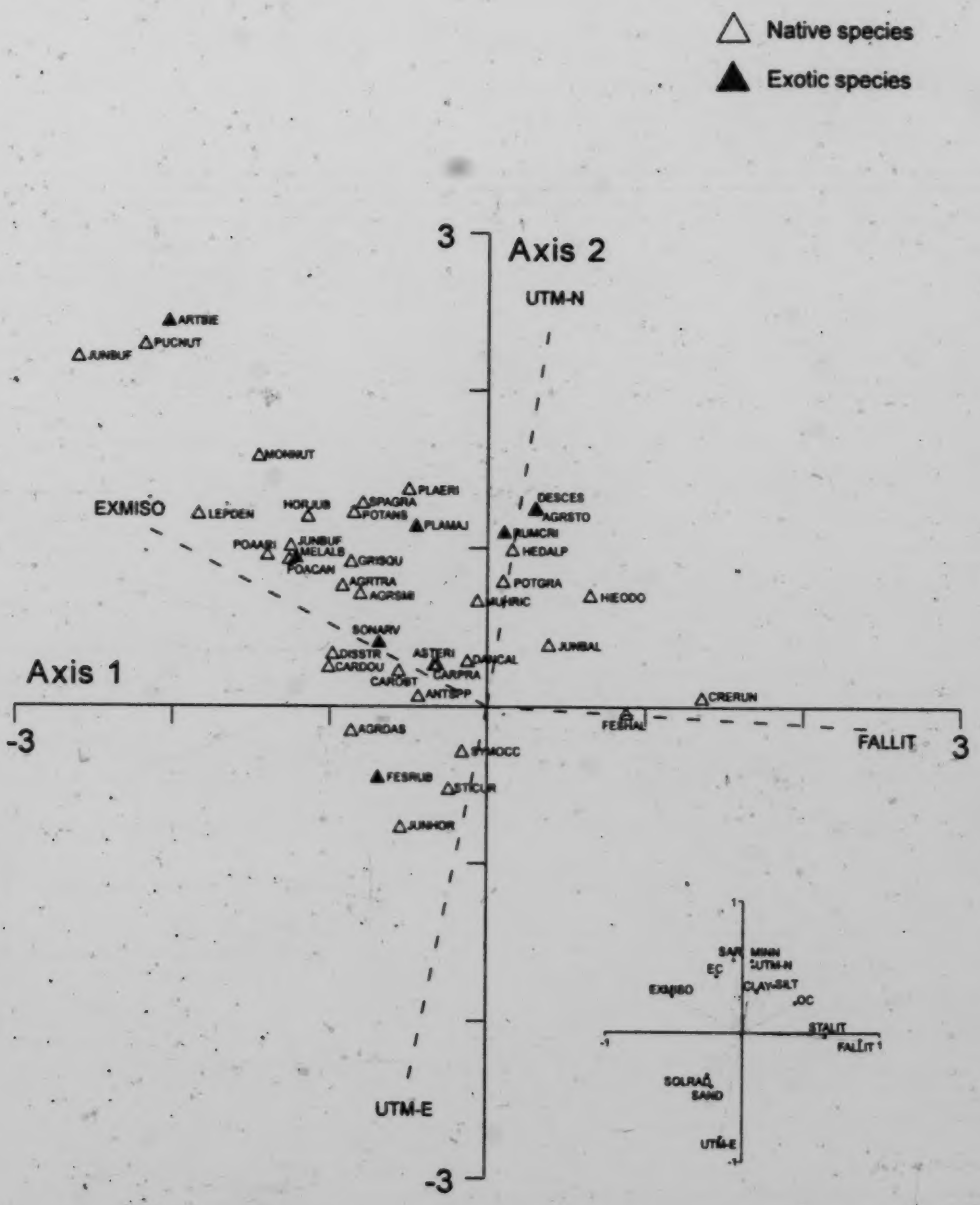

Figure 2-5. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays species tolerant to the moderately to highly sodic or saline soil conditions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

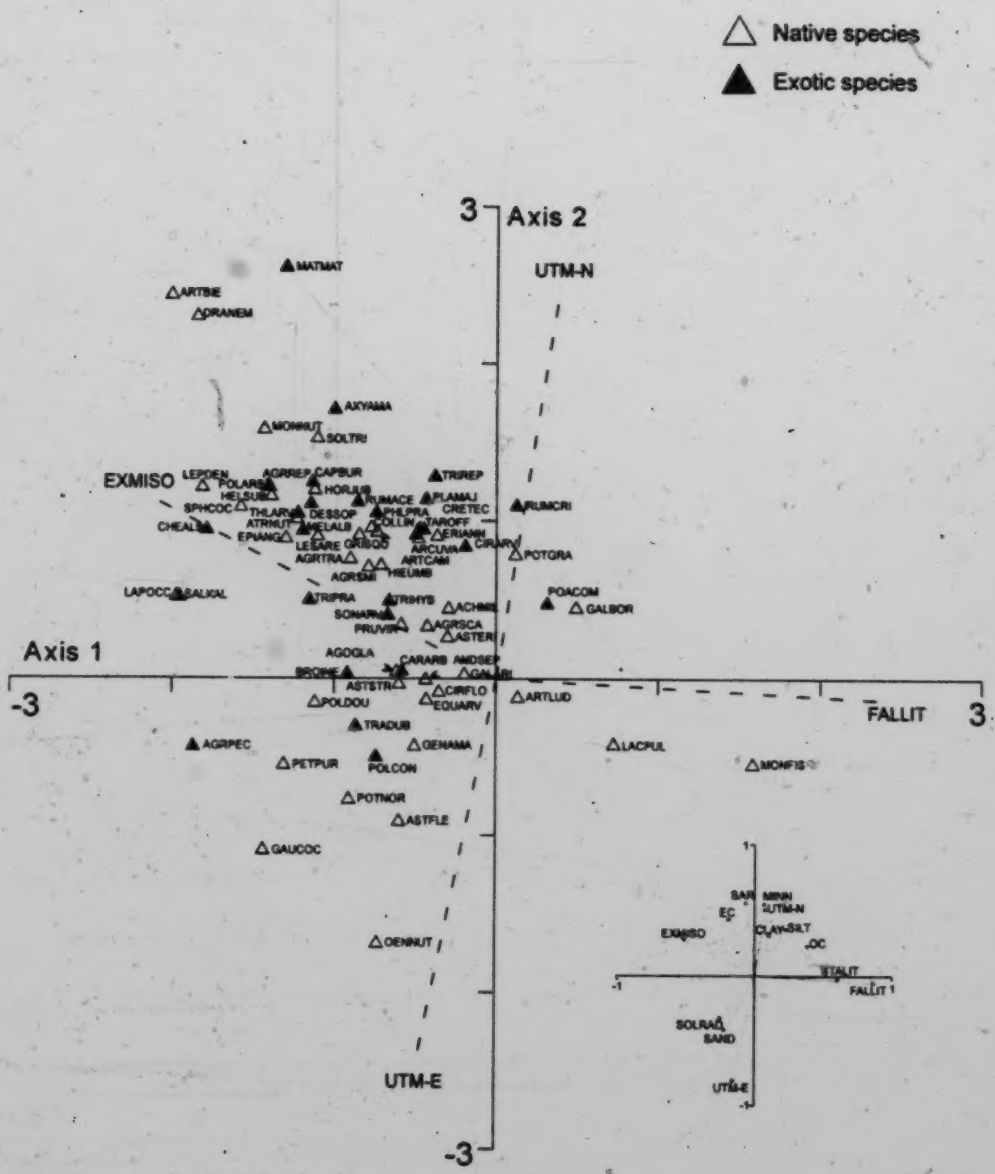

Figure 2-6. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays species often found on disturbed ground. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

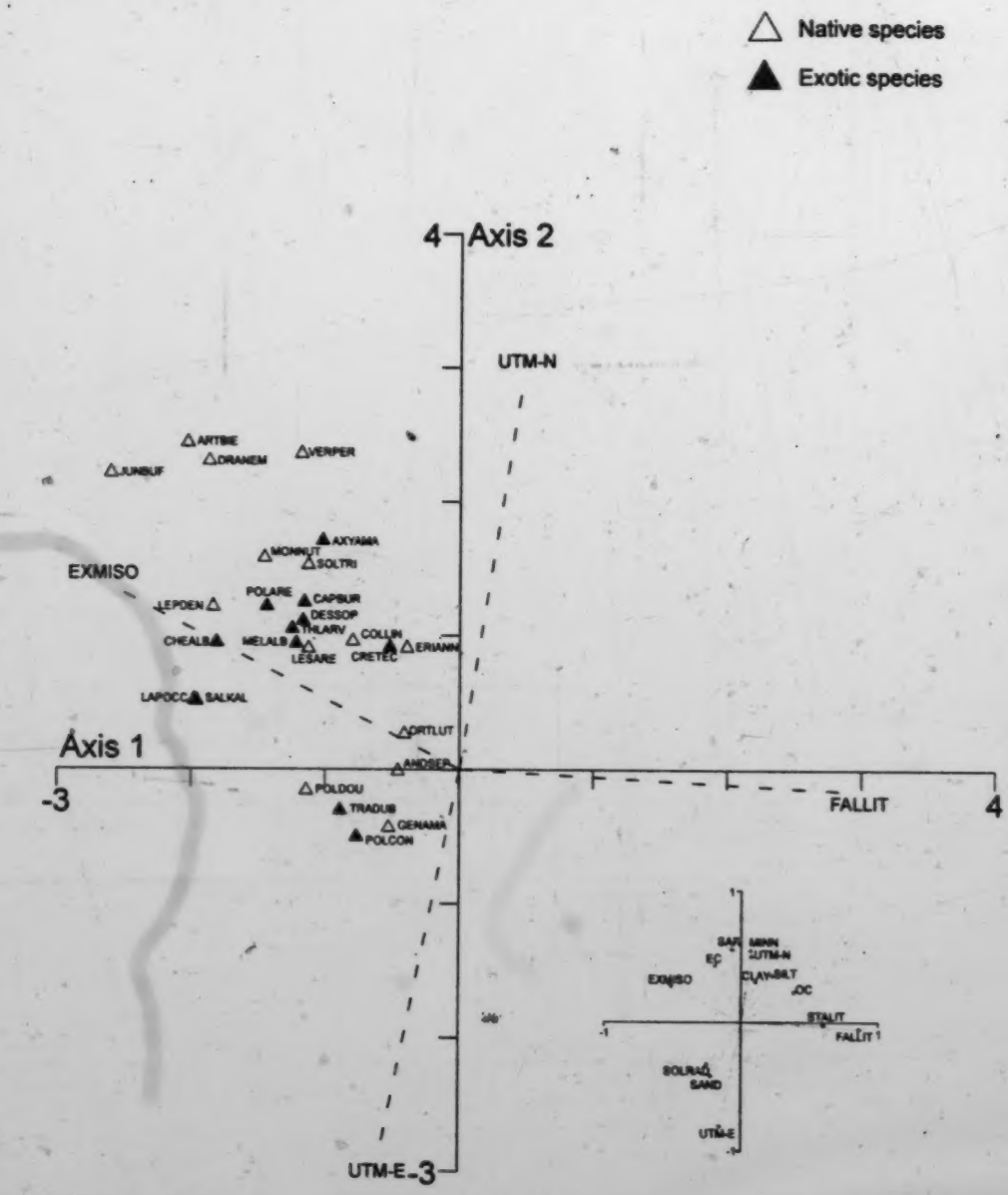

Figure 2-7. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays annual life forms only. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

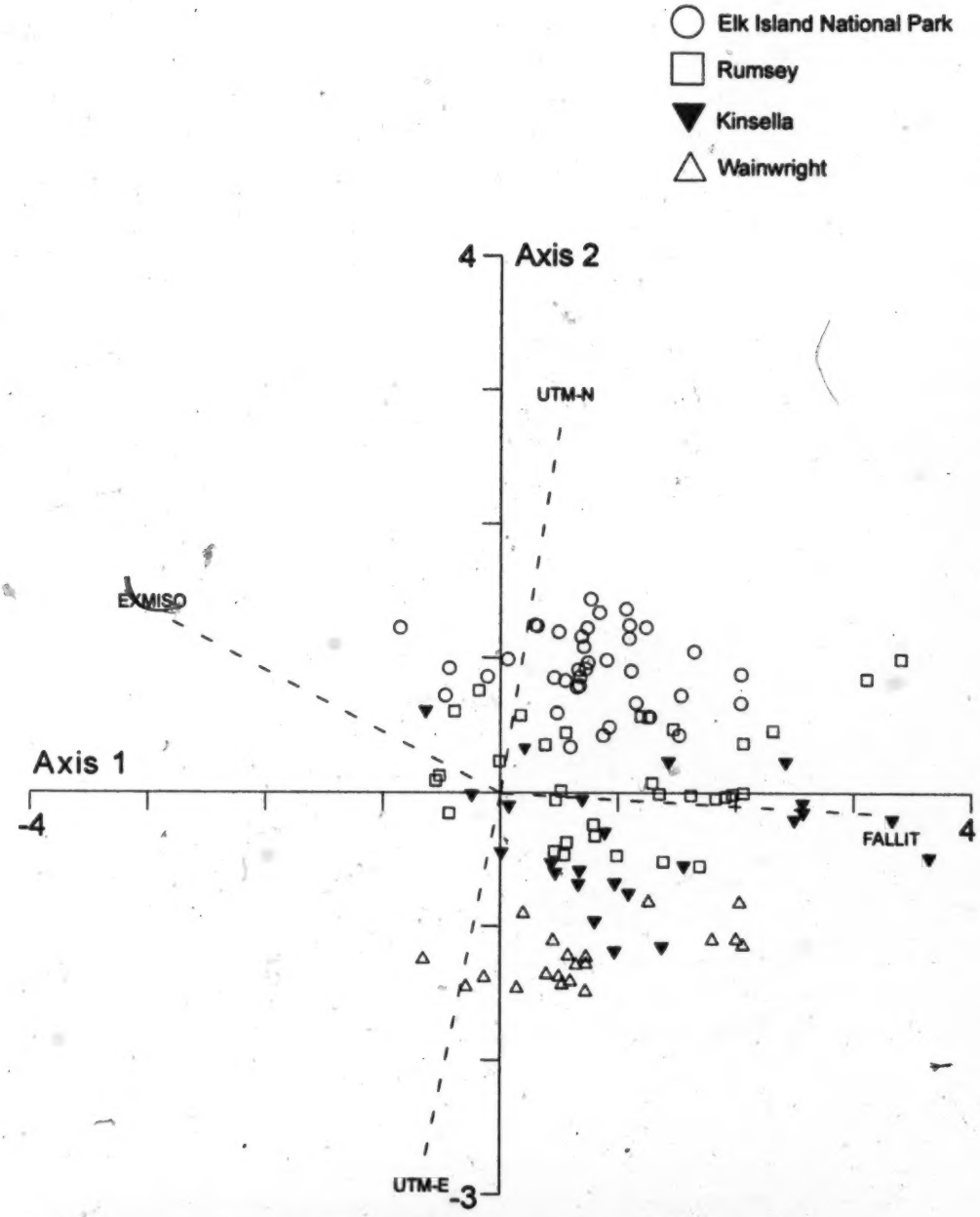

Figure 2-8. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group A derived by UPGMA. Different symbols represent four geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

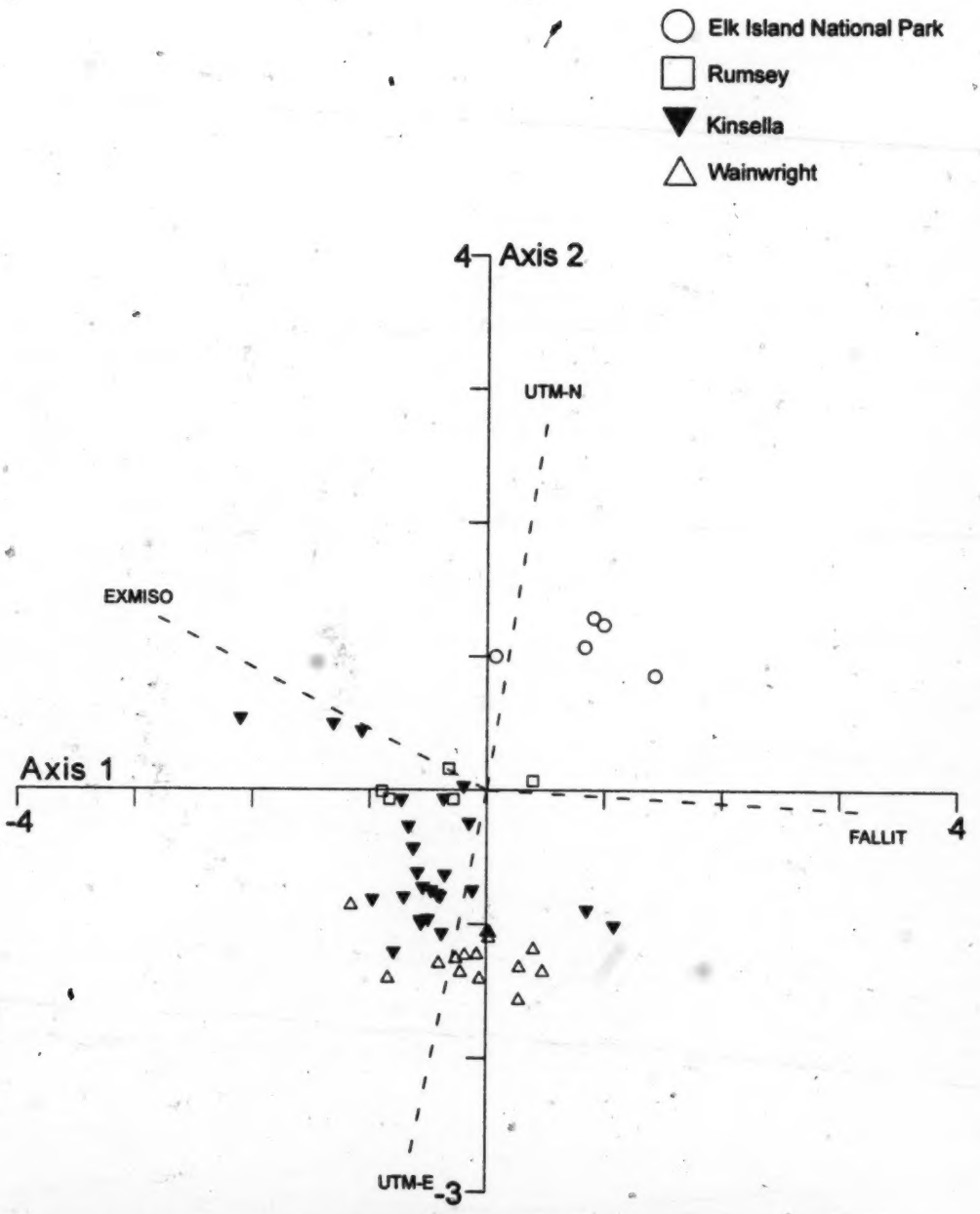

Figure 2-9. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group B derived by UPGMA. Four symbols represent four geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

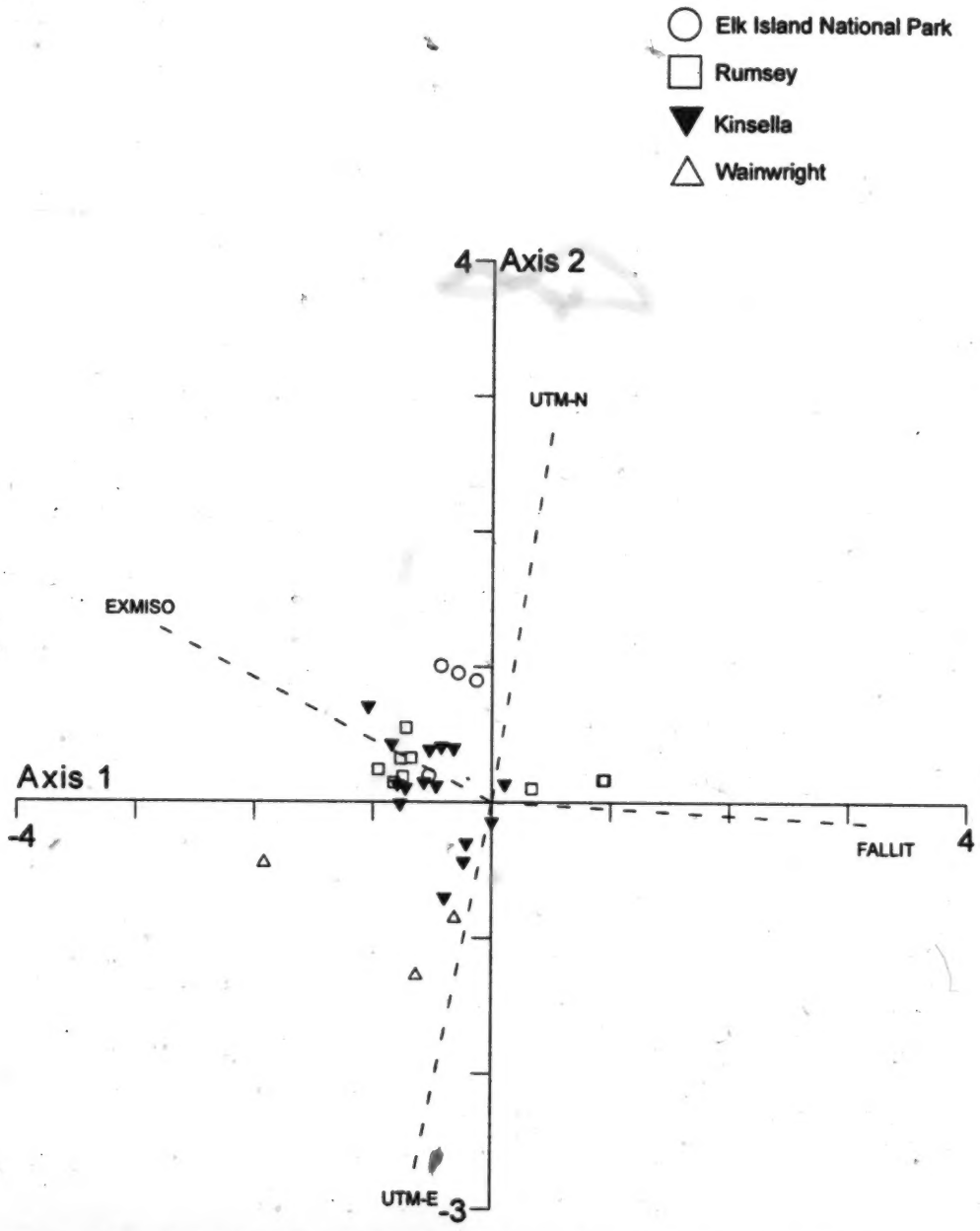

Figure 2-10. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group C derived by UPGMA. Four symbols represent four geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

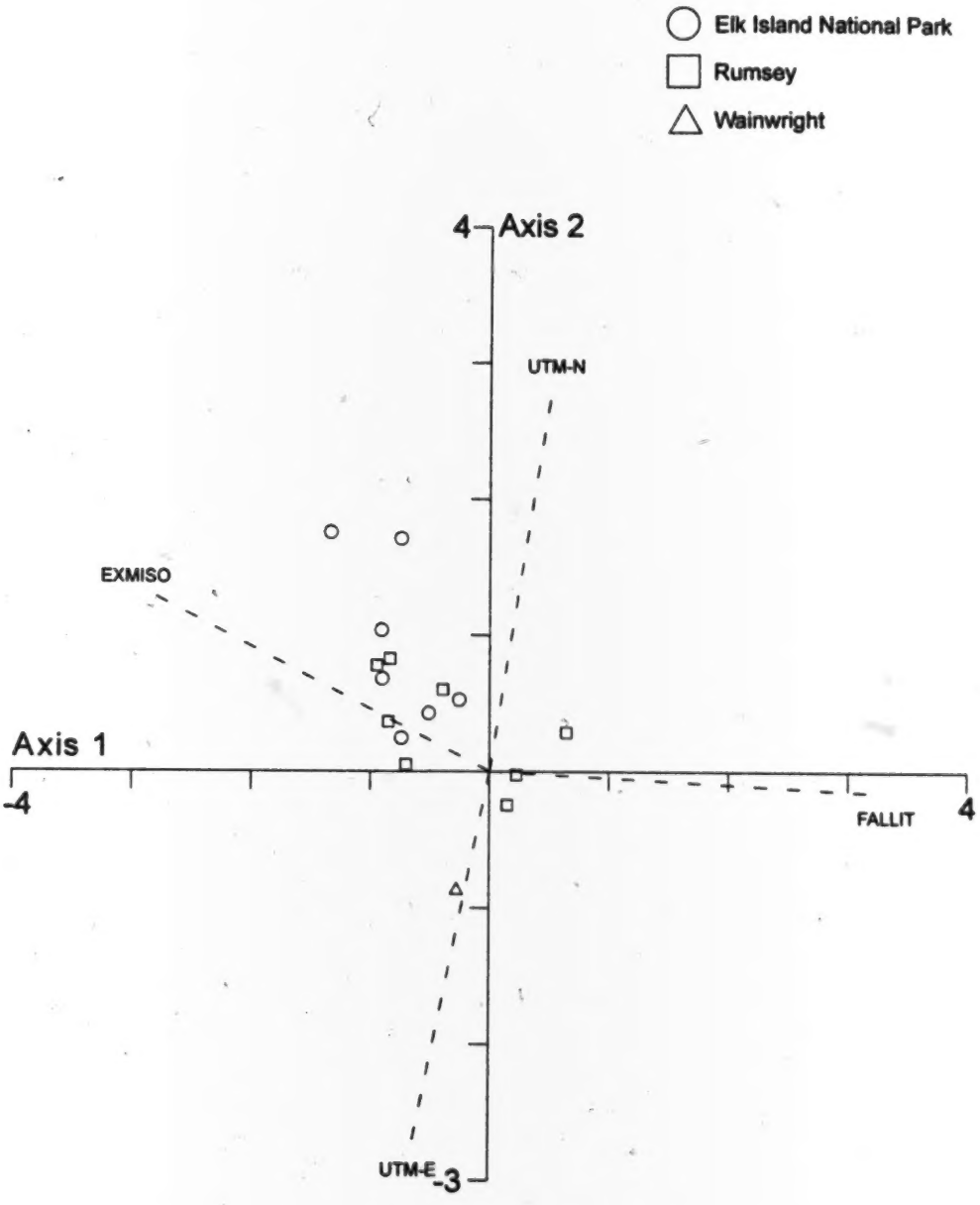

Figure 2-11. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group **D** derived by UPGMA. Three symbols represent three geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

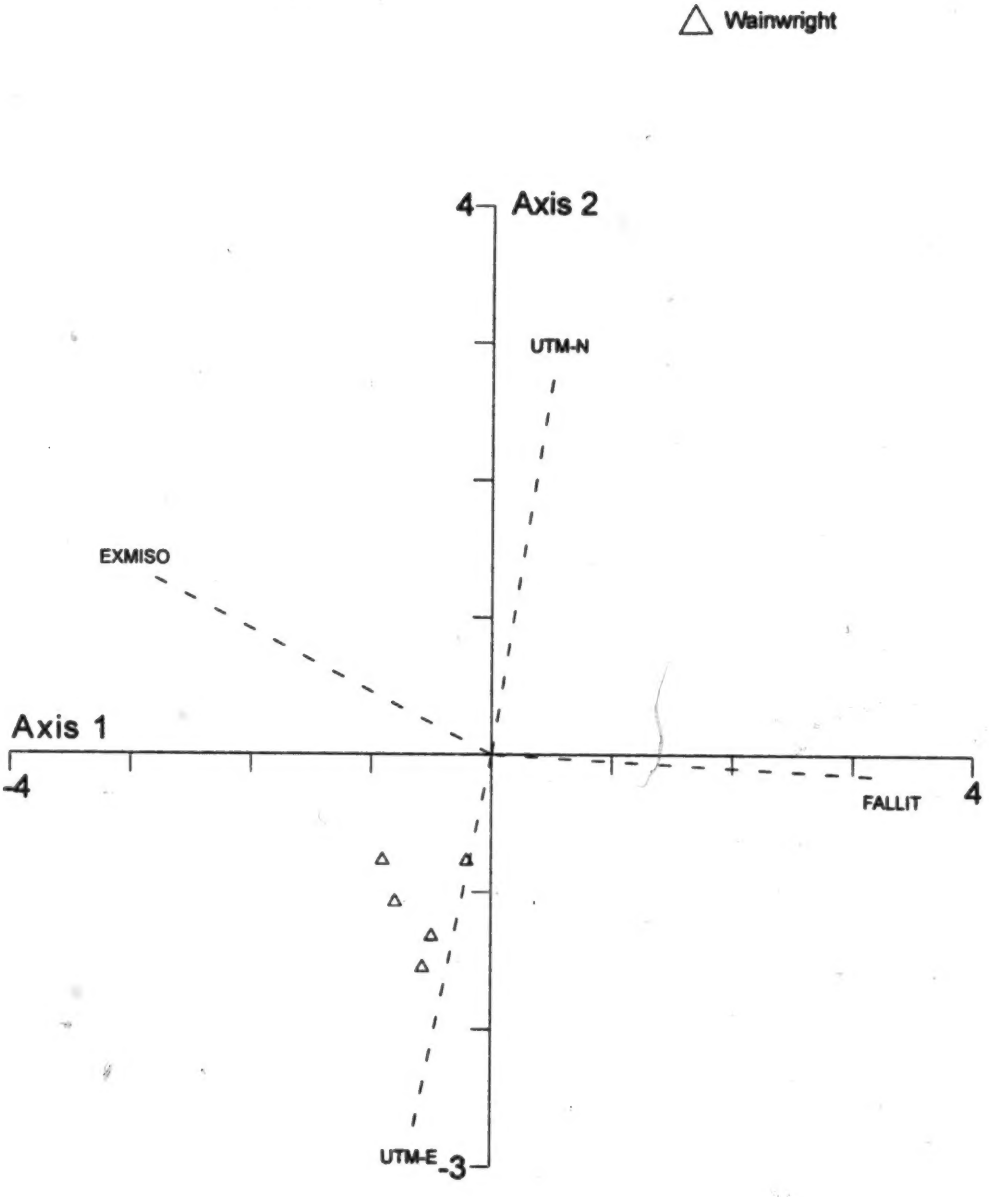

Figure 2-12. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group E derived by UPGMA. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

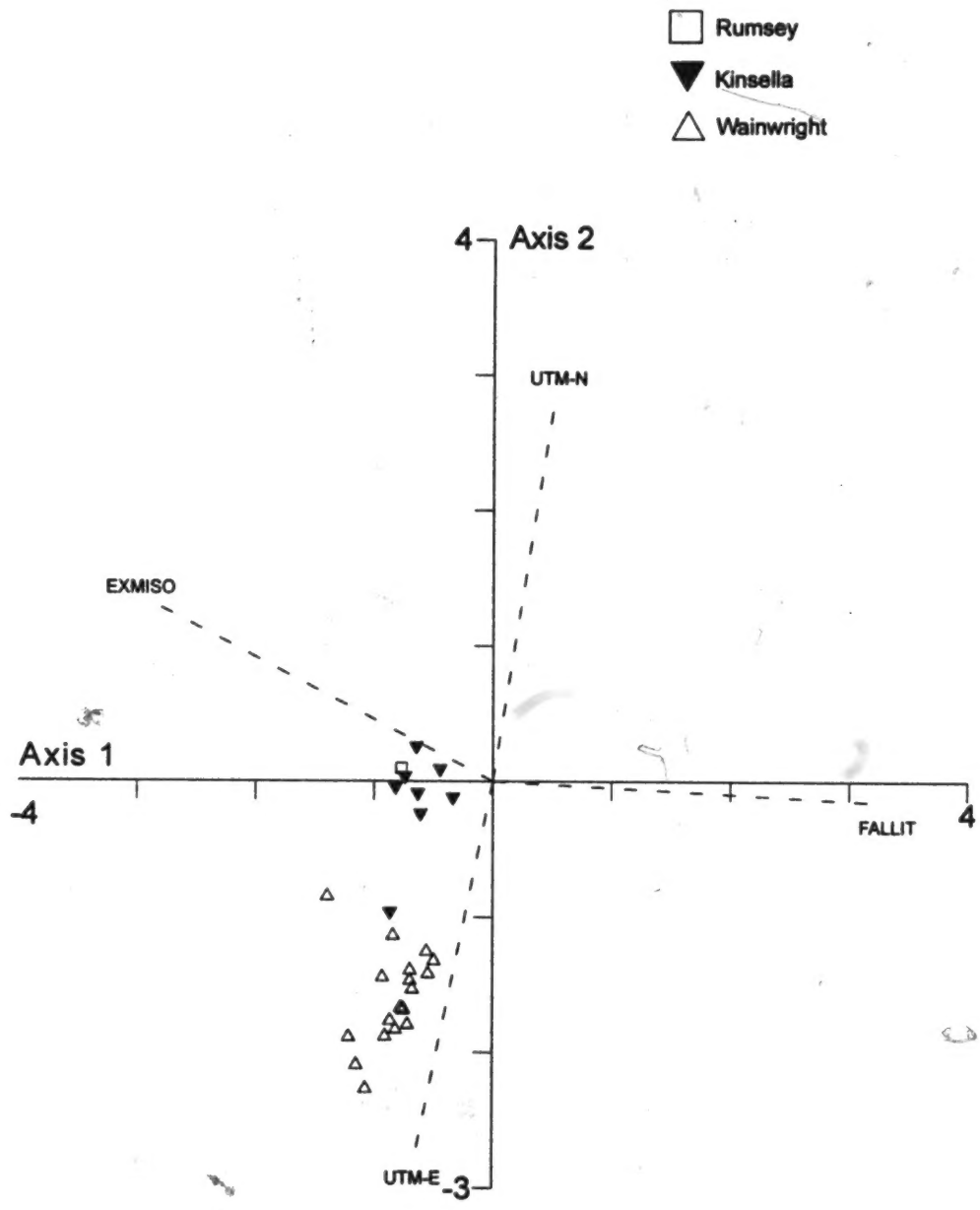

Figure 2-13. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group **F** derived by UPGMA. Three symbols represent three geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

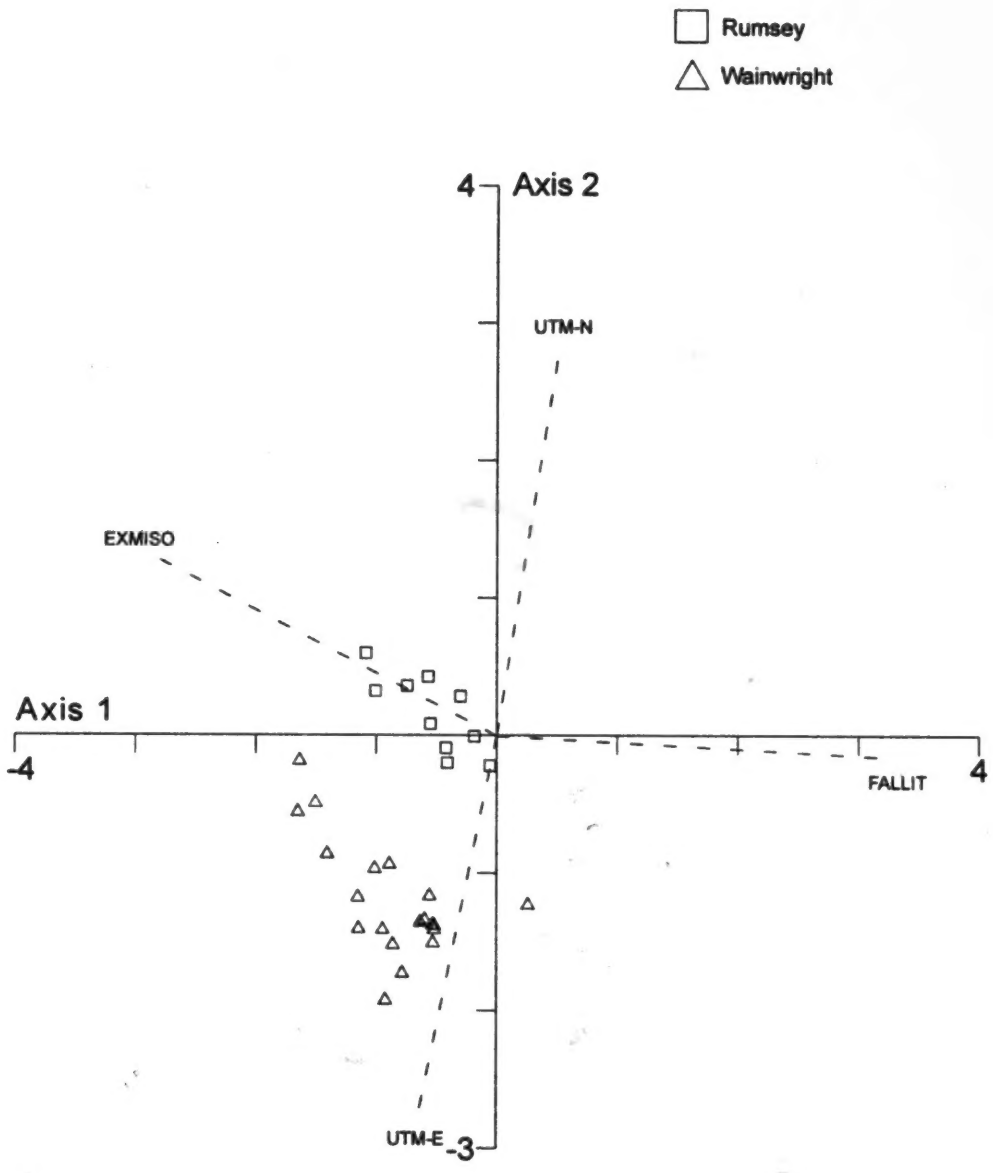

Figure 2-14. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group G derived by UPGMA. Two symbols represent two geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

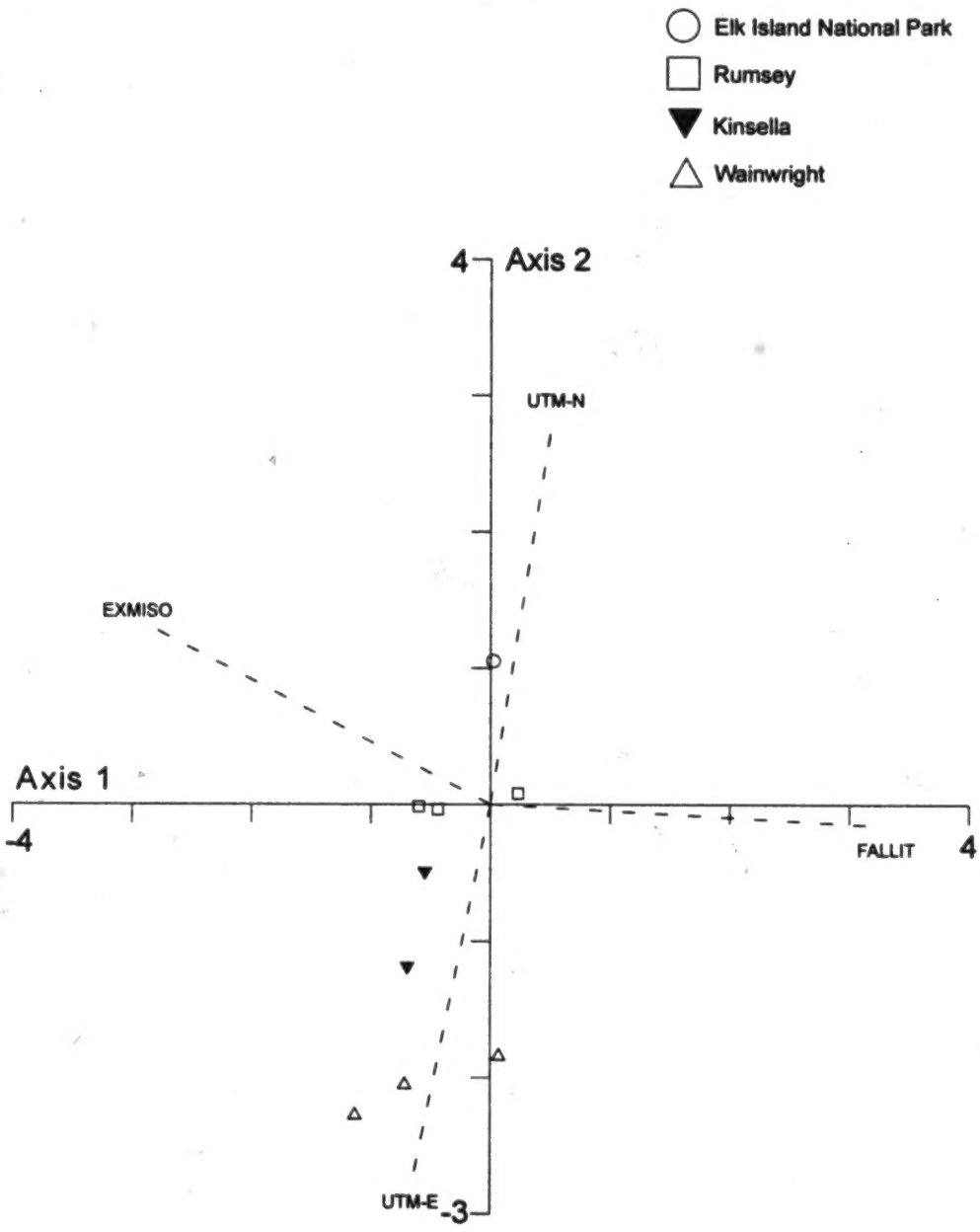

Figure 2-15. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group **H** derived by UPGMA. Four symbols represent four geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

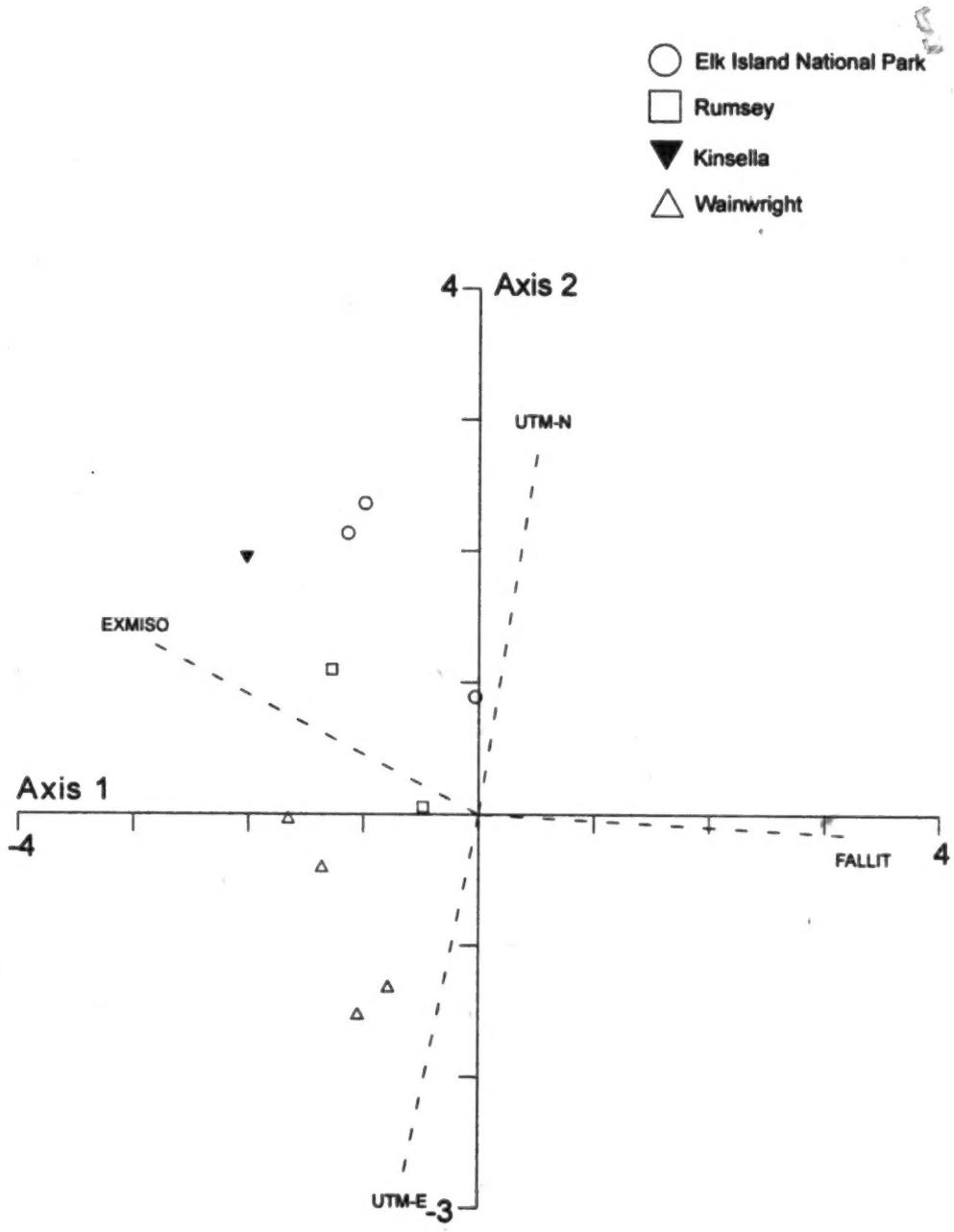

Figure 2-16. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrats group I derived by UPGMA. Four symbols represent four geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

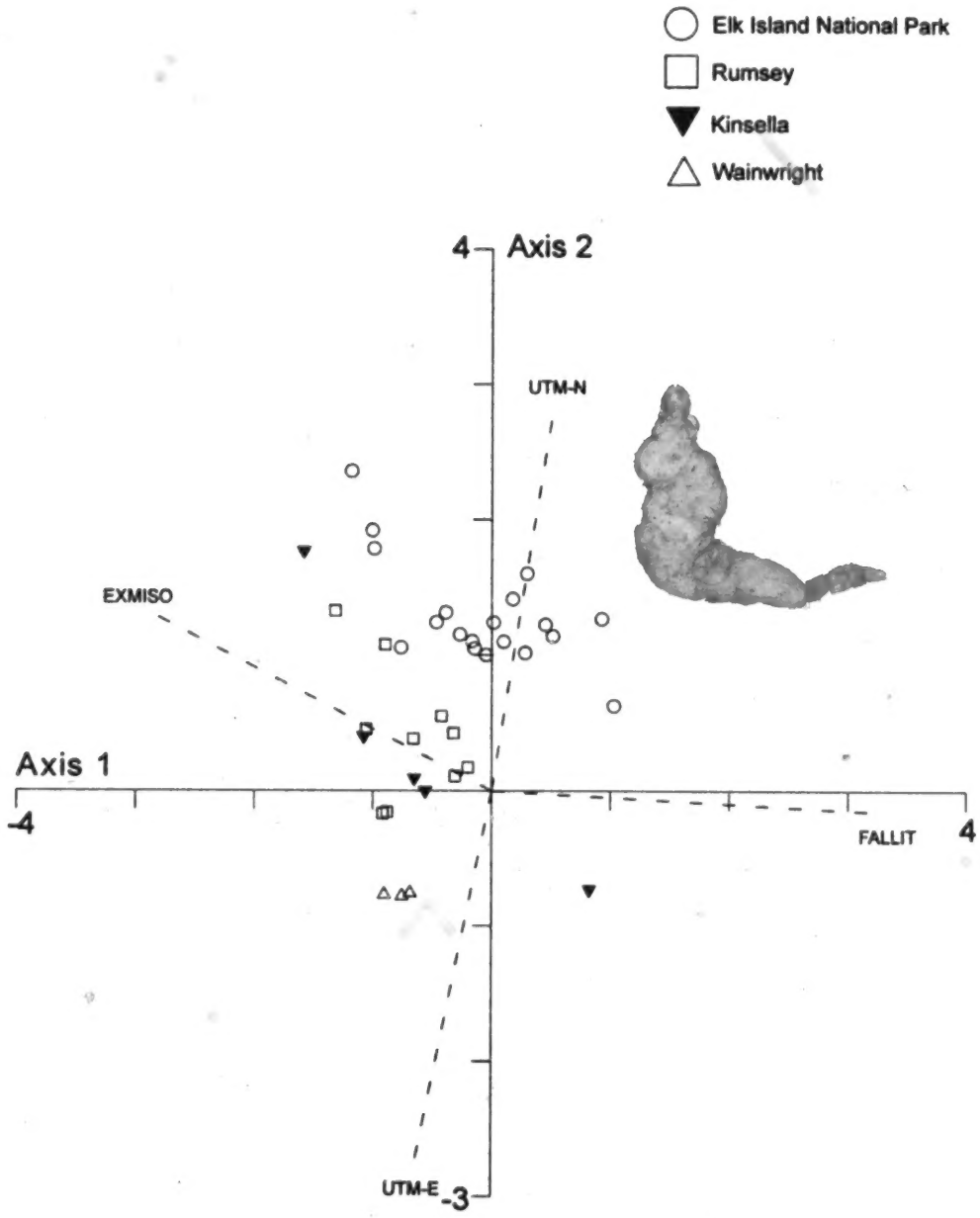

Figure 2-17. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrats group J derived by UPGMA. Four symbols represent four geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

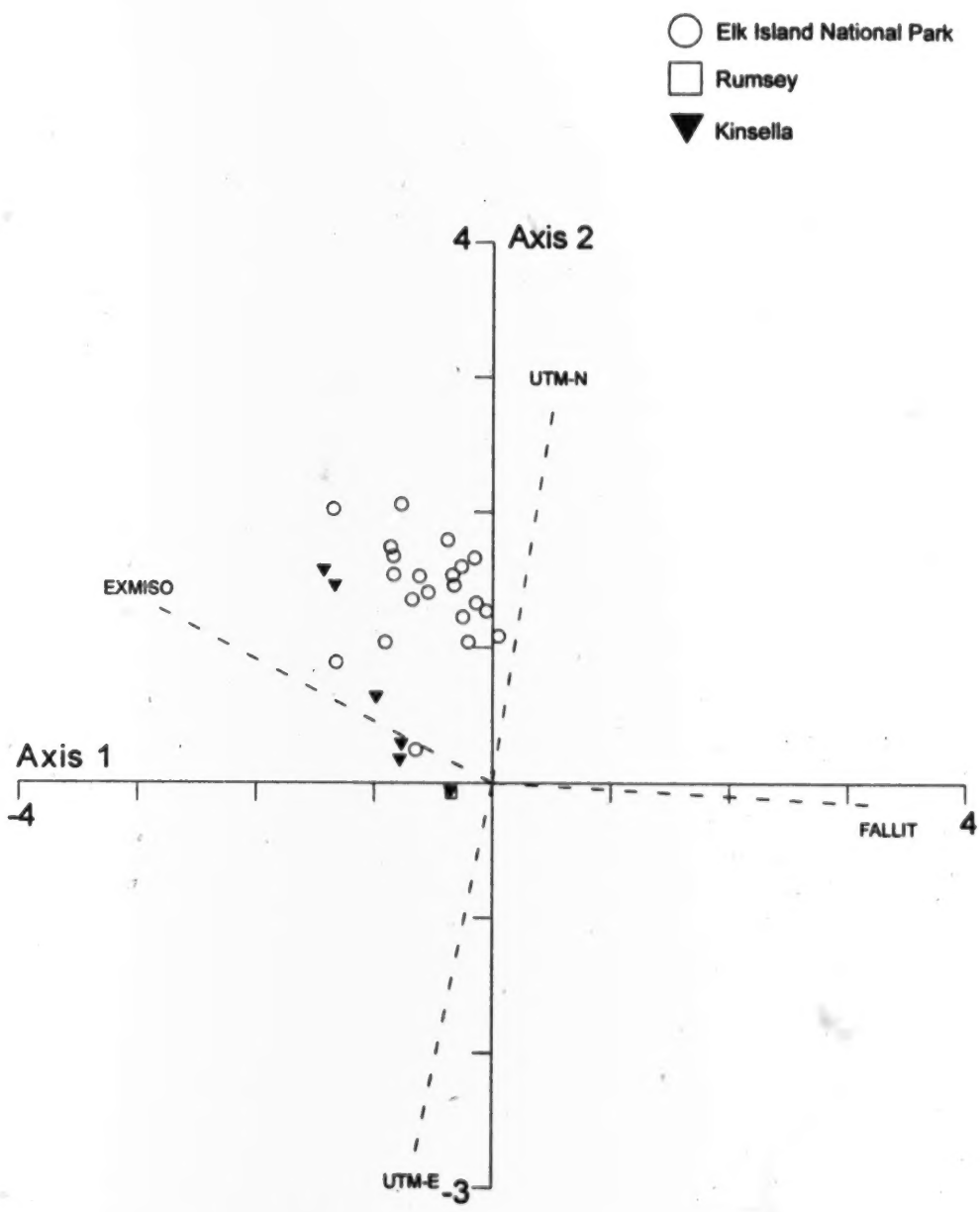

Figure 2-18. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group **K** derived by UPGMA. Three symbols represent three geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

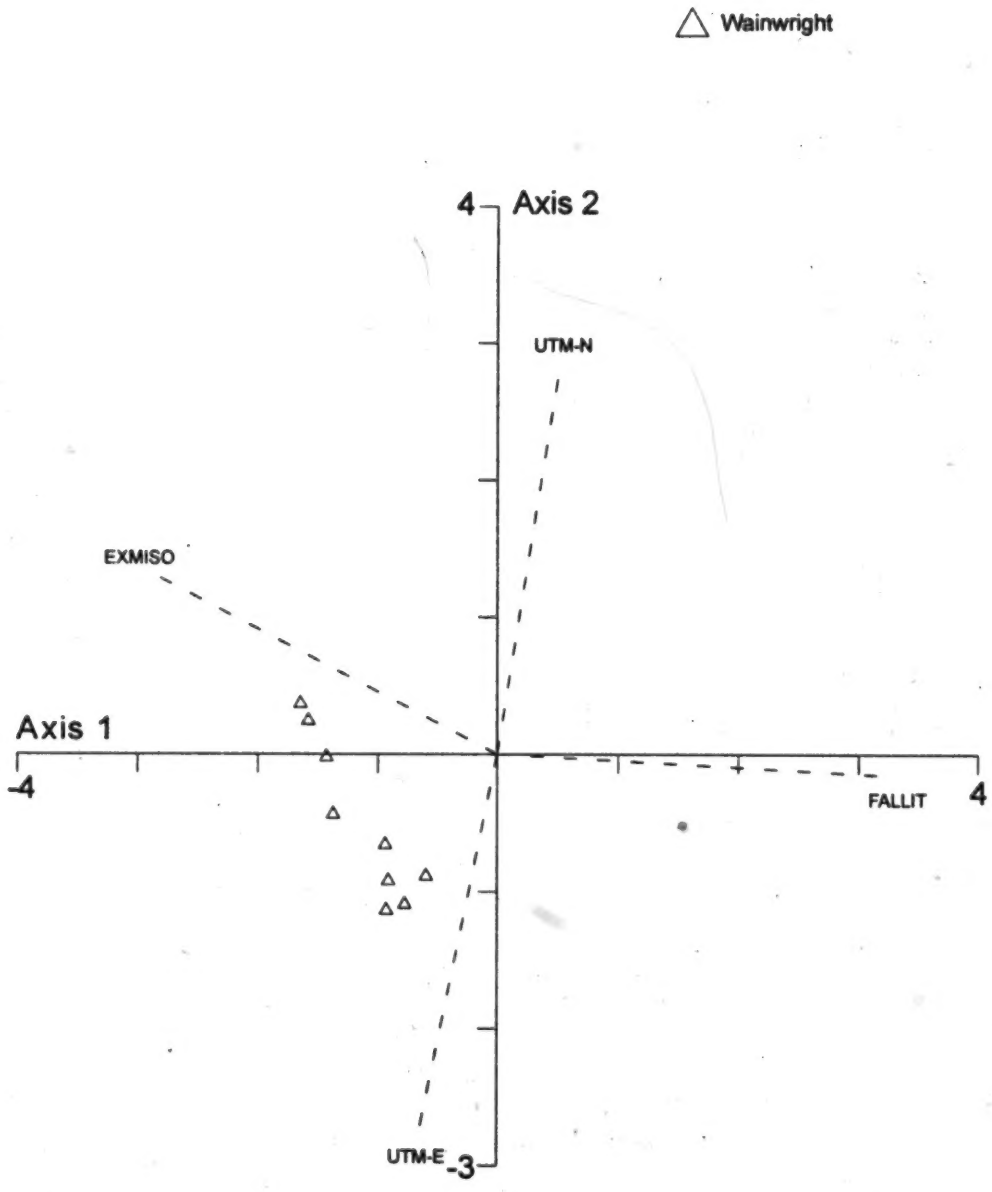

Figure 2-19. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group L derived by UPGMA. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

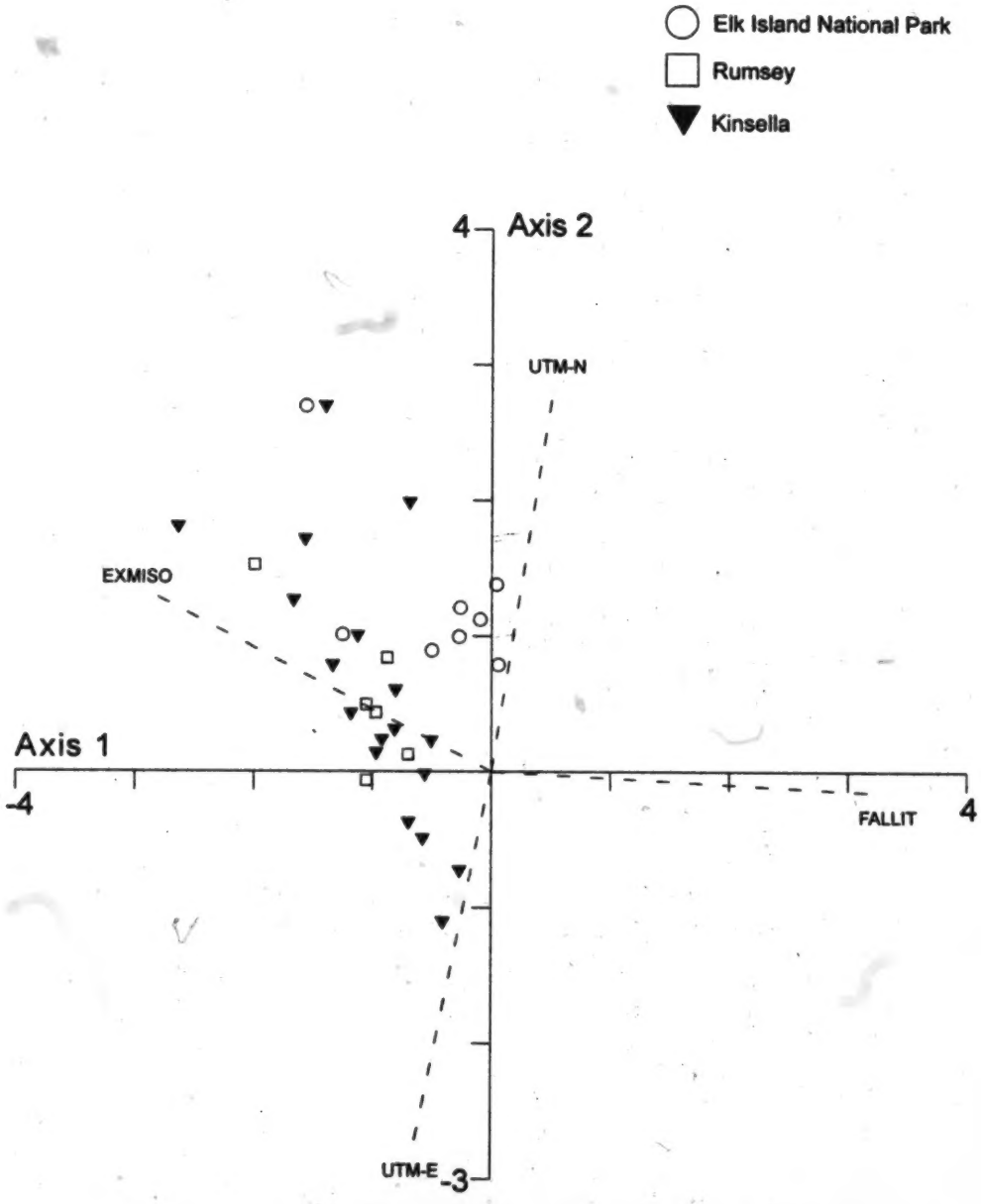

Figure 2-20. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group **M** derived by UPGMA. Three symbols represent three geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

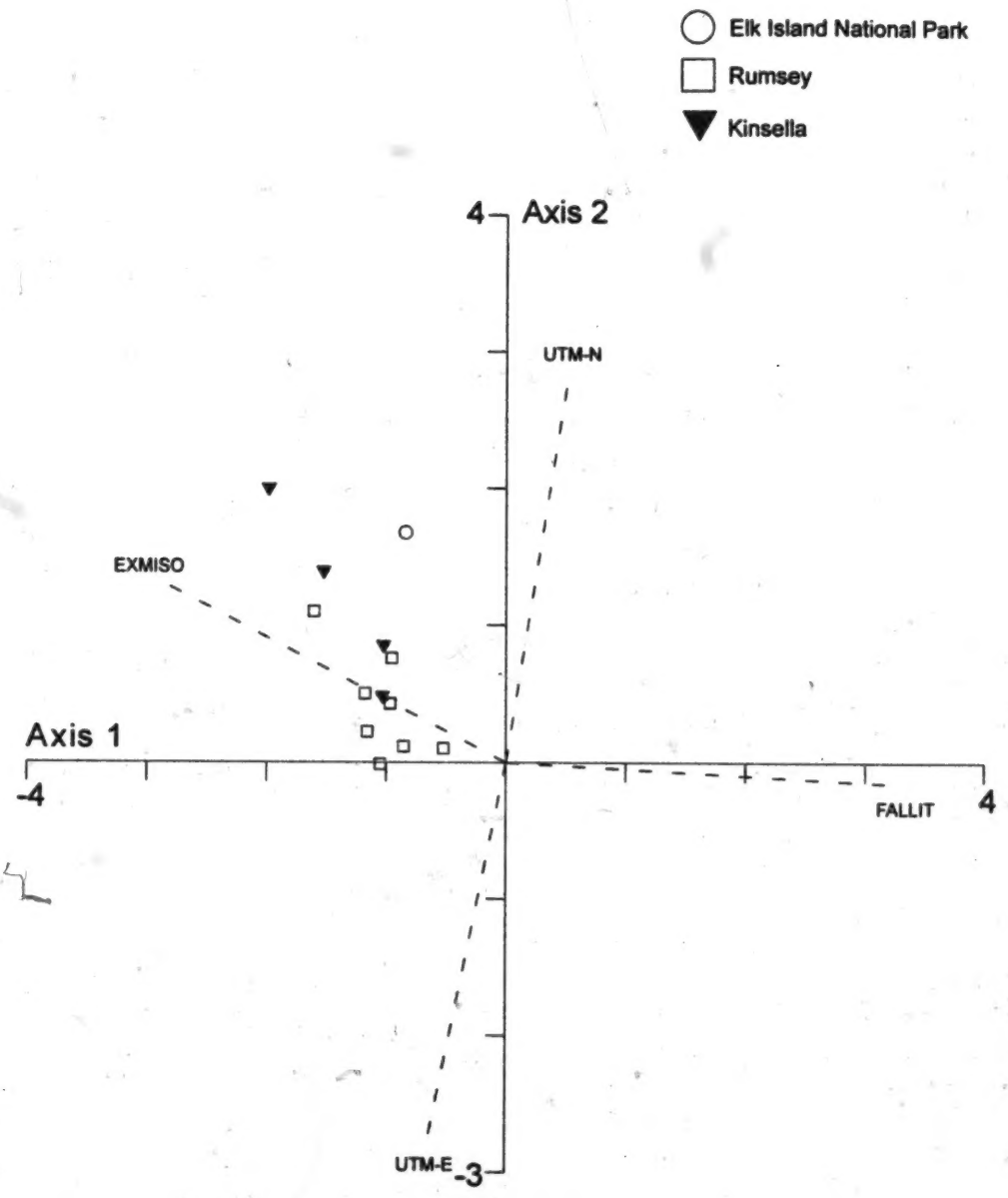

Figure 2-21. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group N derived by UPGMA. Three symbols represent three geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

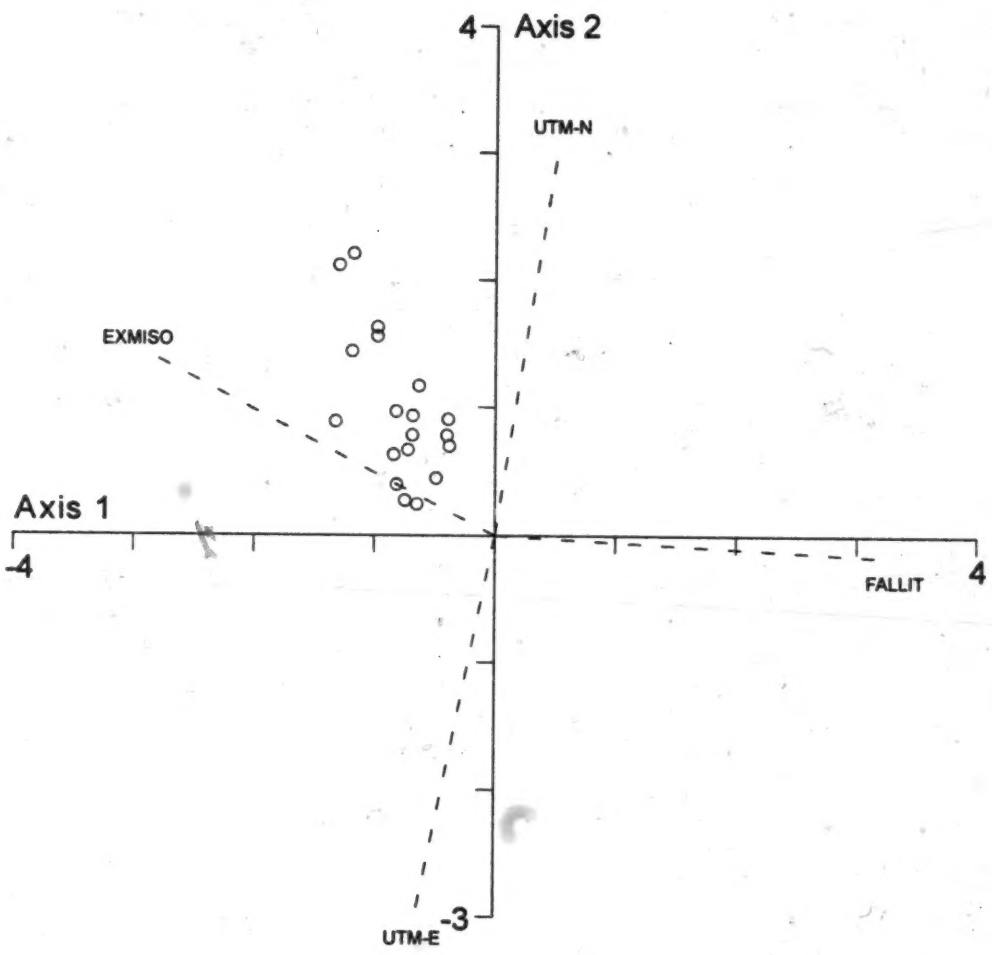

Figure 2-22. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group **O** derived by UPGMA. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

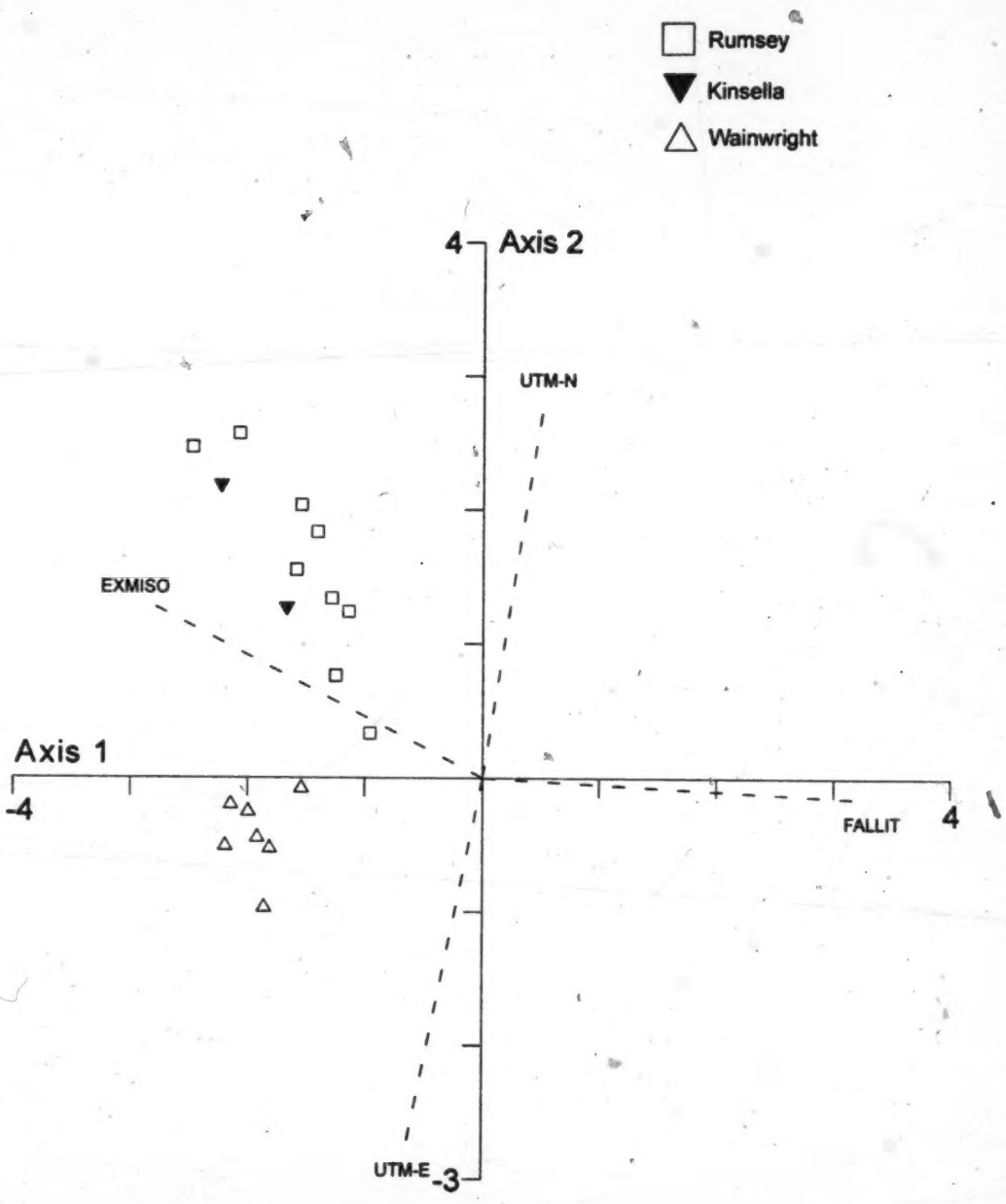

Figure 2-23. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group **P** derived by UPGMA. Three symbols represent three geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

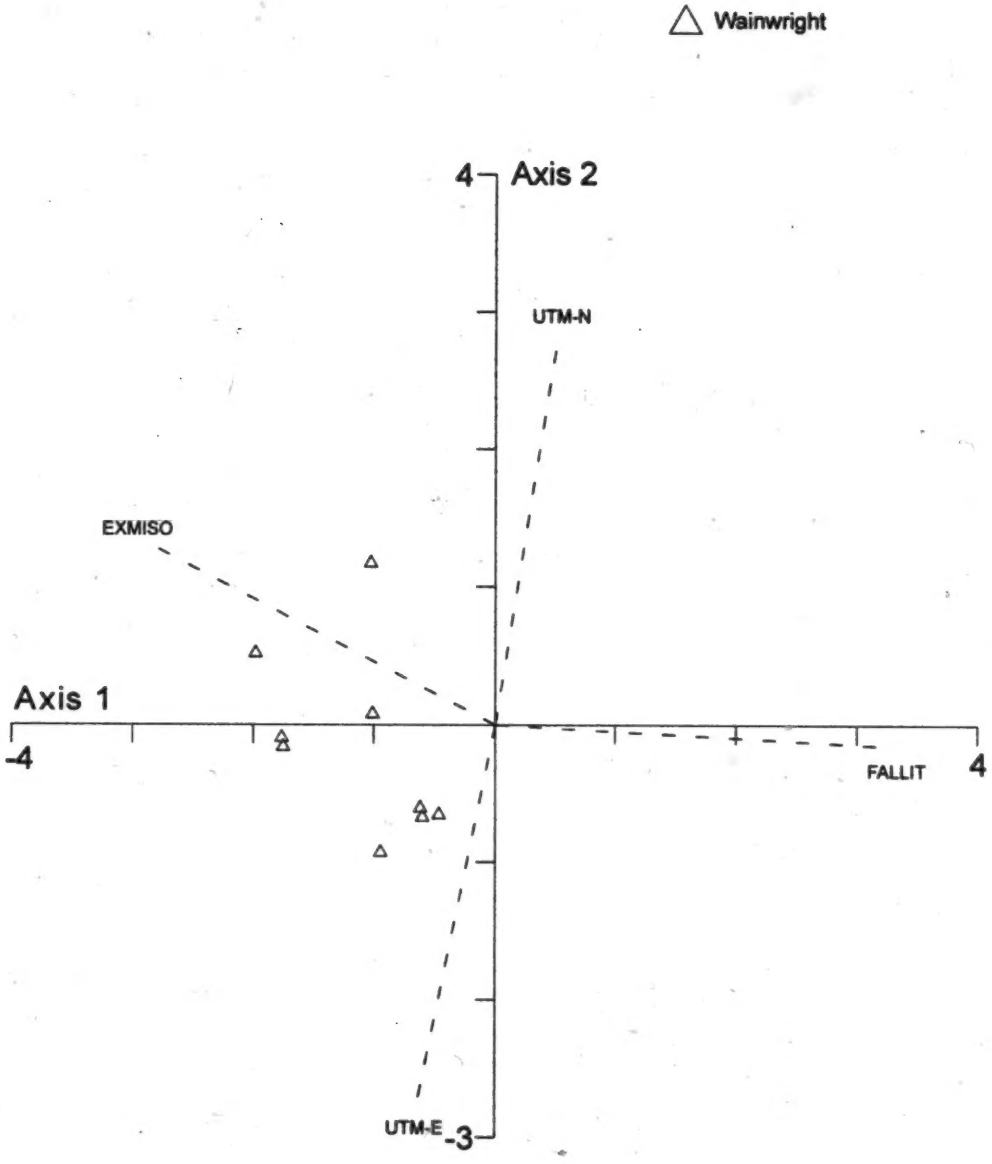

Figure 2-24. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group Q derived by UPGMA. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

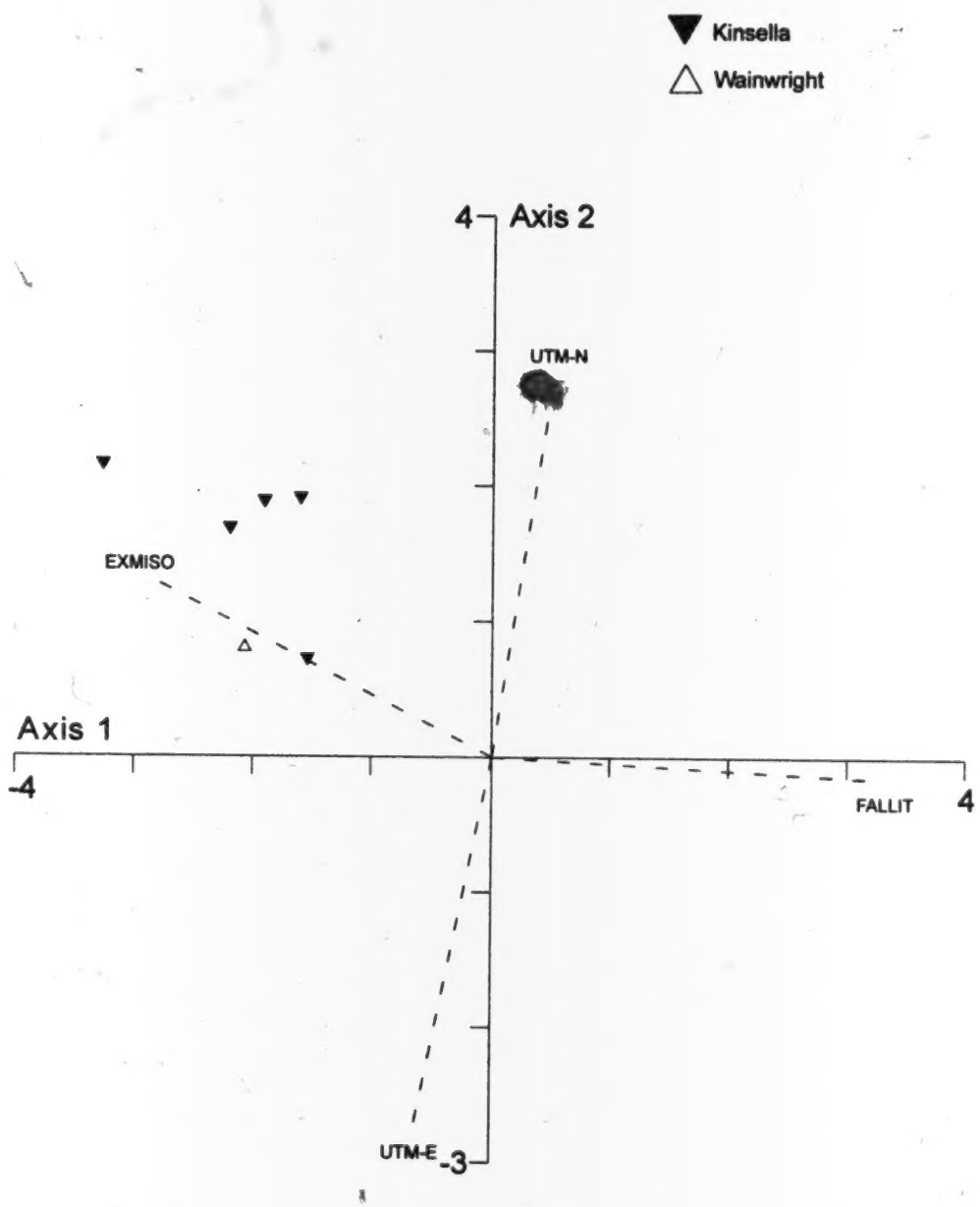

Figure 2-25. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group **R** derived by UPGMA. Two symbols represent two geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

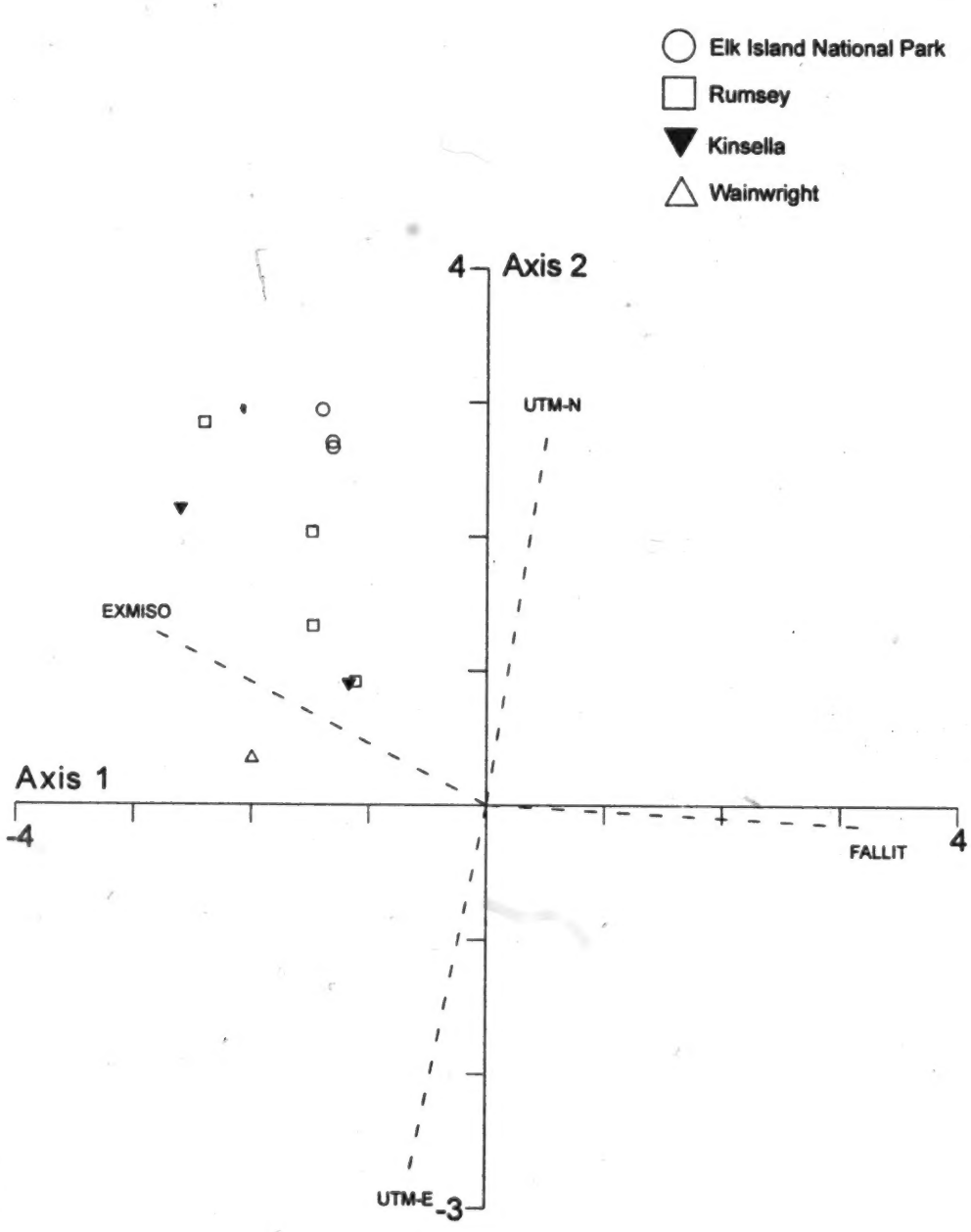

Figure 2-26. Ordination diagram based on CCA-1 of 484 quadrats from remnant grasslands in the aspen parkland. The diagram displays quadrat group S derived by UPGMA. Four symbols represent four geographical regions. In the main diagram the positions of the four major environmental variables are shown, but their lengths are not proportional to their importance.

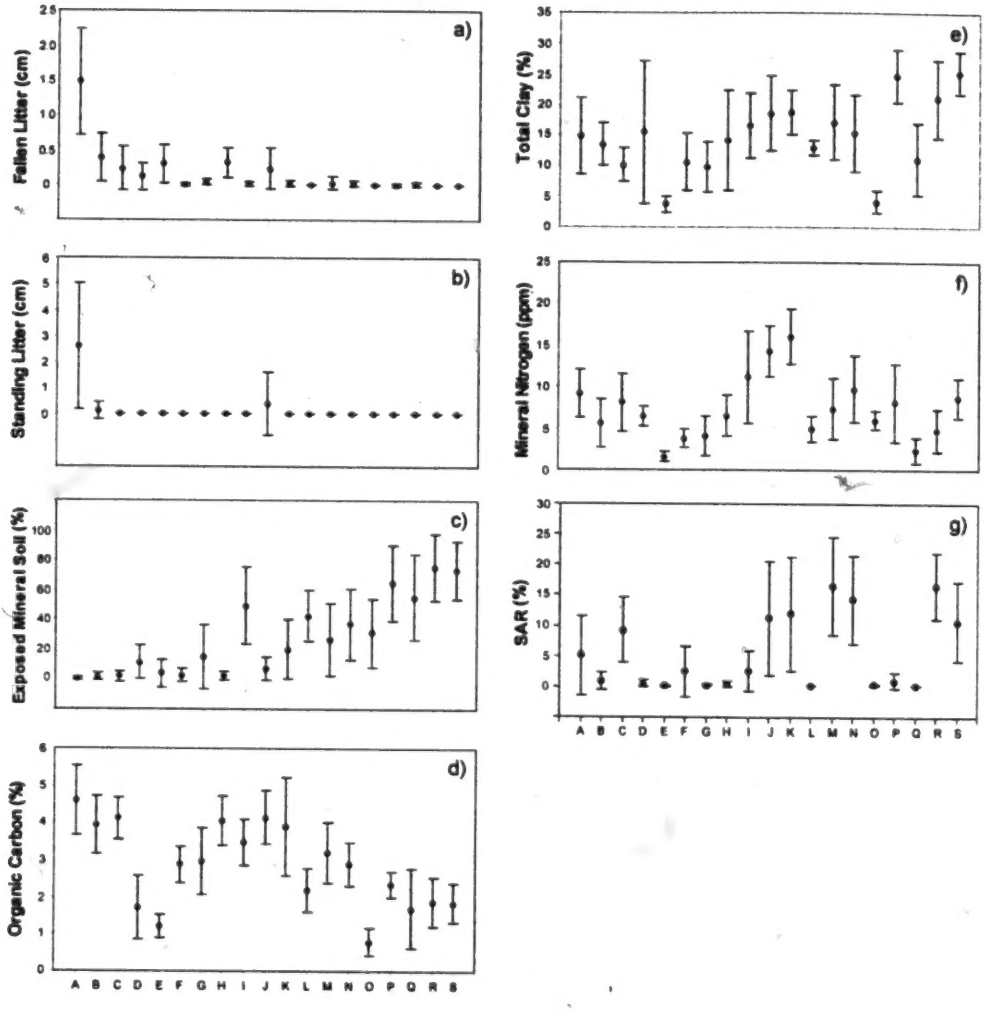

Figure 2-27. Means of the significant environmental variables for each quadrat group (A to S) derived by UPMGA. Error bars are shown for one standard deviation on each side of the mean. Plant species characterizing each quadrat group are presented in Table 2-2. a) mean fallen litter; b) mean standing litter; c) mean exposed mineral soil; d) mean organic carbon; e) mean total clay; f) mean mineral nitrogen; g) mean sodium adsorbtion ratio; h) mean total sand; i) mean solar radiation; j) mean latitude; k) mean longitude.

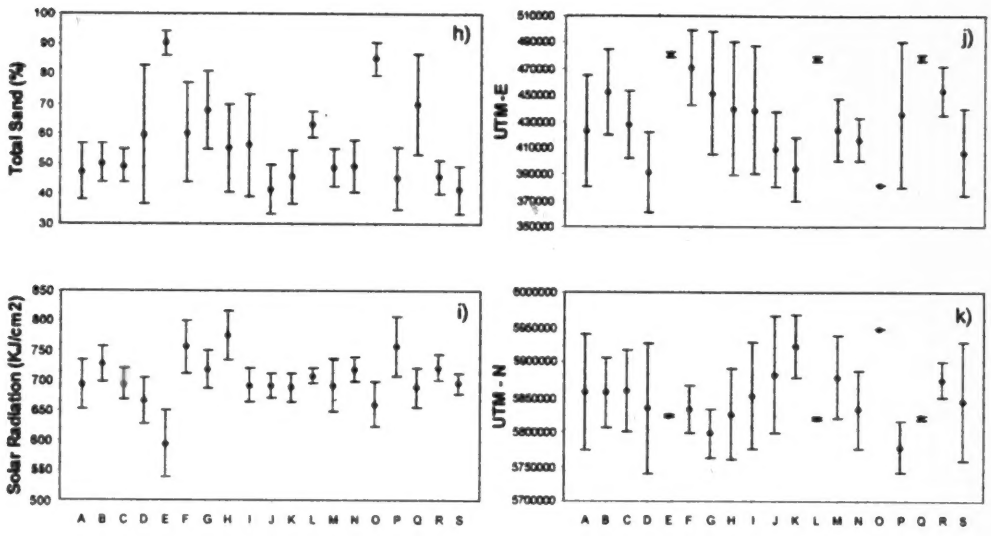

Figure 2-27. Continued.

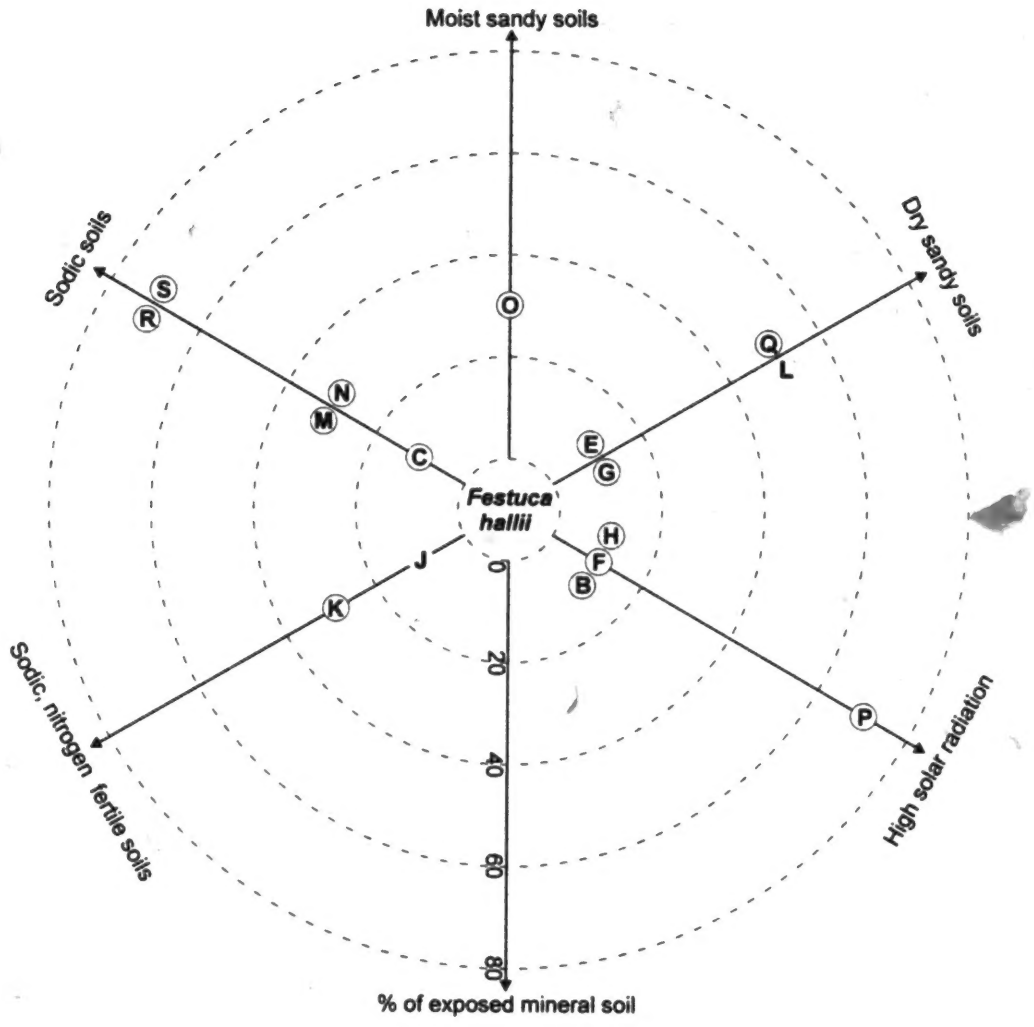

Figure 2-28. Centrifugal organization of quadrat groups (A-S) derived by the UPGMA. Quadrat groups **D** and **I** are omitted from the diagram because they did not show clear position along any of proposed disturbance/environmental gradients. Distance of each quadrat group from the core habitat represents its actual position along disturbance gradient, defined by the % of exposed mineral soil. Names of vascular plants characterizing each quadrat group are presented in Table 2-2.

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CHAPTER 3

A TEST OF THE INTERMEDIATE DISTURBANCE HYPOTHESIS IN REMNANT PRAIRIE GRASSLANDS

Introduction

In native plant communities, disturbances are a major source of spatial and temporal heterogeneity as well as an agent of natural selection (Sousa 1984). Sousa (1984) defined disturbance as "discrete, punctuating killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals to become established". Two other frequently used definitions for disturbance are those from Grime (1979) and Picket and White (1985). Similarly to Sousa's definition, Grime (1979) defined disturbance as "a mechanism that limits the plant biomass by causing its partial or total distraction". Picket and White (1985) referred to the opening in space, change in the availability of light, and soil nutrients as disturbance, indicating that it does not have to represent direct physical injury to the living organism.

Numerous authors have discussed the impact of large-scale physical disturbances (large waves, storms, fire, high winds, and drought) on different plant communities (Sousa 1984, Picket and White 1985). Others have explored biological disturbances resulting from grazing or digging by small mammals (Platt 1975, Collins and Glenn 1988, Martinsen *et al.* 1990). Generally, it has been shown that the diversity of plant species can be associated with the level of habitat disturbance. The "Intermediate Disturbance Hypothesis" (IDH) states that the greatest species diversity occurs in the medium range of disturbance (Connell 1978), where species coexistence is maintained at a non-equilibrium state and no strong competitor can become completely dominant. The hypothesis has been of considerable theoretical interest since it was proposed (Connell 1979, Grime 1979, Huston 1979, Collins and Glenn 1988, Petraitis et al. 1989, Keddy 1991, Jorgensen and Padisak 1996, Bartha et al. 1997, Collins and Glenn 1997). Three aspects of disturbance have often been discussed separately in relation to species diversity: (1) disturbance frequency, (2) time interval since the last disturbance, and (3) magnitude of the disturbance ("a measure of the damage caused by the distracting force" *sensu* Sousa

1984) (Connell 1978, Connell 1979, Huston 1979, Abugov 1982, Sousa 1984, van der Maarel 1993). Connell (1978) suggested that species diversity will be the highest if both frequency and magnitude of disturbance are intermediate or in the midpoint of succession when temporal scale must be considered. The author also proposed that the highest species diversity will exist when disturbances are intermediate in size ("the amount of area disturbed per disturbance event" *sensu* Petraitis et al. 1989). However, Petraitis et al. (1989) argued that there is no evidence for the sensitivity of species diversity only to size of the disturbance.

In addition to the variety of disturbance types and aspects (frequency, time, magnitude, size) described in the literature with regards to the IDH, there is a variety of spatial scales at which the IDH has been tested. When originally proposed (Connell 1978), the IDH pertained exclusively to the species diversity within a disturbed patch of 1 m^2 (α-diversity or within-patch diversity). A patch represents "a continuous area in which the effect of a disturbance is uniform and the subsequent dynamics are similar" (*sensu* Petraitis et al. 1989). However, numerous studies have tested the IDH at two other scales, β-diversity (between-patch diversity) and γ-diversity (landscape-scale diversity) (Huston 1996).

The most extensive testing of the IDH has been done in aquatic (Connell 1979, Sousa 1979, Padisák *et al.* 1993, Sommer 1995) and terrestrial non-grassland ecosystems (Grubb 1977, Connell 1978, 1979, Burns 1995, Hiura 1995, Parikesit *et al.* 1995, Stone and Wolfe 1996, Yoshimura et al. 1997). Few authors have tested the hypothesis in grassland ecosystems. The latter examined the effects of grazing (Collins and Glenn 1988, Bowers 1993, McIntyre and Lavorel 1994), soil disturbances (Platt 1975, Martinsen et al. 1990, McIntyre and Lavorel 1994, Kotanen 1995, Guo 1996), and fire (Collins and Glenn 1988, Collins 1992, Collins *et al.* 1995) on species diversity. Results of the IDH testing from different grassland types are not consistent, whereby the outcome of each study may depend on the type of disturbance under investigation and to the range of disturbances considered. Grime (1973) and Martinsen *et al.* (1990) warned that studying only one kind of disturbance at a time (e.g., grazing, fire, or mowing) and

having only a small range of disturbance levels (three or four) may not provide the full range of levels of disturbance required for the proper testing of the IDH. Despite acknowledged problems with the test of the IDH, Reynolds *et al.* (1993) and Reynolds (1995), who extensively tested the hypothesis in phytoplankton communities, summarized the general importance of testing the IDH: "It represents a mature and reasoned expression of the interaction among, on the one hand, the internally driven progress toward energetic equilibrium (*sensu* Odum 1969) and, on the other hand, the externally imposed stochasticity of environmental variables operating at a variety of temporal scales".

There are many reports of a positive relationship between the level of habitat disturbance and the abundance of exotic plants (Fox and Fox 1986, Mooney and Drake 1986); however, the actual importance of exotic species for the diversity at different levels of disturbance has been neglected. Some studies were done in Australian wetlands (McIntyre et al. 1988) and grasslands (McIntyre and Lavorel 1994), Californian prairies (Kotanen 1995), and in the riparian zones in Northern Europe and the United States (Nilson *et al.* 1989, DeFerrari and Naiman 1994, Planty-Tabacchi *et al* 1995, Pyle 1995). Although results, in general, show a positive linear relationship between exotic species richness and disturbance levels, the inconsistency in the interpretation of the results suggested that results may depend on the type of disturbance and habitat characteristics under investigation. In addition, Planty-Tabacchi et al. (1995) reported that in agreement with a number of reviewed studies, their results showed a positive linear relationship between total species richness and percent of exotic species. The interpretation of their results from the perspective of the IDH suggests that exotic species may account significantly for the species diversity increase at some medium range of a disturbance gradient. Finally, Hobbs and Huenneke (1992) emphasized that understanding of the relationship between disturbance and native and exotic species diversity can influence management decisions on what disturbance regime is required to preserve natural plant communities.

The majority of studies on diversity and disturbance in grasslands considered vascular species diversity only, with no reference to non-vascular, moss, and lichen species. Although studies on the response of non-vascular plant diversity to disturbance have been poorly represented in the literature, there are some published data that suggest dependence of non-vascular species diversity in grasslands on the disturbance regime. Watson (1960) and Wells et al. (1976) related the decrease in diversity of moss and lichen species in England chalk grasslands to the exclusion of selective grazing by rabbits. Similar results were obtained for Dutch chalk grasslands that were protected from grazing by sheep (During and Willems 1986). On the other hand, heavy anthropogenic disturbances may also result in low moss diversity (Belland and Brassard 1988, Belland and Schofield 1994).

Objectives

The objectives of this part of the study were to test the hypotheses that (1) the greatest within-patch plant species diversity (for vascular plant species alone and plant species in total) will occur at intermediate levels of disturbance range; (2) the richness of exotic vascular plants will show a positive relationship with disturbance levels; and (3) exotic vascular plant species will be mainly responsible for a disproportionate amount of the total vascular species diversity at the intermediate disturbance levels.

Methods

Field sampling

Sampling of vegetation data (percent cover for all vascular and non-vascular species) was conducted from July to August 1996 when most species were phenologically well developed (for details on study area refer to Chapters 1, 2). Briefly, 490 quadrats of 1 m^2 size were selected by stratified randomization so that all disturbance types present at a site could be included (Figure 1-4, Chapter 1). Each quadrat was given one of the following descriptions regarding the type of the disturbance: (1) no vegetation or soil disturbance; (2) light grazing with no soil compaction; (3) moderate grazing with low soil compaction; (4) heavy grazing with moderate soil compaction; (5) farm tracks or cow paths with high soil compaction; (6) more than two year old mixing of soil; (7) up to two

year old mixing of soil; (8) removal of up to 10 cm of topsoil; (9) removal of 10-30 cm of topsoil; and (10) removal of more than 50 cm of topsoil. The presented order of disturbance classes (in ascending magnitude of disturbance) was assigned based on the degree of plant biomass removal and the degree of the structural alteration of the soil caused by different disturbances. Sampling of each disturbance type was conducted as described in Chapter 1.

Data analyses

To arrange all ten types of disturbance more objectively, a correlation test was performed among ten proposed disturbance codes and 13 environmental variables sampled at each plot (for variables sampled see Chapter 2). The highest correlation (0.73) was between proposed disturbance classes and percent exposed mineral soil. Percent of exposed mineral soil has also been used as an indicator of the level of habitat disturbance by Martinsen *et al.* (1990). For each disturbance category described, the mean percent of exposed mineral soil for all quadrats was determined and then the disturbance categories were reordered in increasing order of percent exposed mineral soil. The new order of disturbance classes was: 1, 2, 3, 6, 4, 5, 8, 10, 7, 9 (Table 3-1).

Reordering of disturbance classes based on exposed mineral soil also provided a correction for the time interval since the last disturbance. Mowing proposed level 6, 8, and 10 to the left on the scale, possibly reflected a longer time interval since the last disturbance. As Connell (1979) suggested, combination of both the time since the last disturbance and the magnitude of disturbance will influence the diversity of species, so that diversity will be the highest if the magnitude of disturbance is intermediate and in the midpoint of succession.

Species Richness (S), Shannon's diversity index (H'), Evenness (E), Hill's Diversity Number (N1), and H'-corrected (the last index will be explained later) were calculated for the data set containing vascular plant species alone, and for the data set that also included non-vascular plants. No attempt was made to test the diversity of non-vascular species alone, because of a higher sampling error when compared to the vascular species

alone. Notes on non-vascular plant species description and percentage cover were made in the field, representative samples were collected, and later identified. However, either because of their small size or the high similarity with other non-vascular plant species, the number of non-vascular species per quadrat found during the identification process frequently exceeded the number of species described for the same quadrat in the field. This indicates that a number of other species could have been missed during the collection in the field. For specimens found only in the laboratory, percent cover was estimated based on their relative abundance in the sample collected for the identification only. In addition, more than 15% of non-vascular plant species (compared to 1% for vascular plants) could only be identified by genus due to the lack of reproductive structures. Despite the problems encountered, I felt that the inclusion of non-vascular with vascular plants in the analyses can provide important information regarding the total diversity of plant species in relation to small-scale disturbances in remnant grasslands, since this aspect had been neglected in previous studies.

The use of the number of species (S) as a diversity measure has been criticized (e.g., Rojo and Cobelas 1993), but it was the measure used when the original hypothesis was proposed (Connell 1978) and it is still one of the indices employed in numerous studies. Shannon's diversity index (H') is based on information theory and it includes both richness and evenness of species (Shannon and Weaver 1963). This index was calculated as:

$$H' = - \Sigma p_i \ln p_i,$$

where p_i was the fraction of the total amount of the sample represented by the ith species, and ln represents the natural logarithm. Shannon's diversity index increases with both richness and evenness and assumes large values when there is a high number of equally represented species. It is one of the most widely used indices in community ecology; but, Ludwig and Reynolds (1988) point out that the same H' can be obtained from a community with high richness and low evenness as well as from a community with low richness and high evenness. Hence, by calculating H' only, it is impossible to ascertain the relative importance of species richness and evenness. One of the solutions to the problem is to determine richness and evenness separately for the same data set and then

use both to interpret the species diversity. Evenness was calculated by the formula proposed by Pielou (1975):

$$E = H'/\ln S$$

where S represented species richness. Evenness (E) expresses H' relative to the H' "maximum" that would be obtained when each species is represented by only one individual (lnS).

Calculation of H'-corrected differed from the provided formula for H' only in that the percent of exposed mineral soil as a "pseudo-species" was added to the list of the species for each plot prior to the calculation of the diversity index. In theory, it influences mostly the assessment of species diversity at high levels of the disturbance gradient, which are characterized by a high percenage of exposed mineral soil. On the other hand, H' of undisturbed quadrats lacking the exposed mineral soil should not be affected and no significant effect on quadrats with high expected diversity of more or less evenly distributed species should be observed.

Finally, Ludwig and Reynolds (1988) supported use of the family of diversity indices (namely diversity numbers N0, N1, and N2) presented by Hill (1973), because diversity numbers provide the best ecological interpretation:

$$N0 = S$$

$$N1 = e^{H'}$$

$$N2 = 1/(1-\Sigma p_i^2)$$

where $1-\Sigma p_i^2$ is Simpson's diversity index. Hill (1973) refers to these diversity numbers as to the "effective number of species" in the sample. Hill's diversity number N0 is the number of all species in the sample, N2 measures the number of very abundant species, while N1 falls between the first two by measuring the number of abundant species, while ignoring only the rarest ones. For the present study, N1 was calculated because of its intermediate position between N0 and N2.

The criteria used to assess the exotic status of vascular plant species were these of Moss (1983). There was little doubt about the status of all except one species (*Poa pratensis*).

In case of *P. pratensis*, Moss (1983) suggested that there might be some elements native to central Alberta. However, the majority of North American publications classify *P. pratensis* as an exotic but naturalized species on the North American continent (e.g., Hitchoock and Cronquist 1973, Forcella and Harvey 1983, Baker 1986, Bazzaz 1986, Mack 1986, D'Antonio and Vitousek 1992). Webb (1985) suggested several criteria for presuming the exotic status of plant species. According to this author, if concrete evidence for the native origin of the species (e.g., fossil evidence, historical evidence, data on local genetic variability) is not available, but the plant grows only in more or less disturbed habitats and is being accepted as exotic for numerous adjacent geographical regions, it seems reasonable to assume its exotic status. The preliminary survey of 120 prairie remnants in the Aspen Parkland Ecoregion revealed the presence of *P. pratensis* only in "improved" pastures, heavily grazed areas, and in moist places at the edge of woods (Vujnovic and Wein 1997). Field evidence and qualification of the species in the majority of publications as exotic but naturalized in North America influenced my decision to classify *P. pratensis* as an exotic species in this study.

Only species richness (S_e) was calculated for exotic vascular plants so that their relative importance for the total diversity of species can be assessed; H', N1, and H'-corrected do not have additive properties, therefore, they are not suitable for testing this hypothesis. I also determined the exotic to native species ratio for each quadrat in order to test the hypothesis that exotic vascular plant species will be mainly responsible for a disproportionate amount of the total vascular species diversity at the intermediate disturbance levels.

Examination of normality and homogeneity of variances for the data sets supported the use of polynomial regressions to relate foregoing diversity indices to the disturbance levels; only the best-fitted curve was retained for the interpretation. Forward selection of degree of polynomial regression was tested by the improvement of the fit based on residual sum of squares (Zar 1984).

Results

Richness of vascular plant species changes in agreement with the IDH. The total vascular plant species richness showed a significant relationship with levels of disturbance, and a third order polynomial regression provided the best fit (R^2= 0.23, P<0.001) (Figure 3-1). The highest species richness existed at intermediate levels of the disturbance range, represented by medium grazing, old mixing of soil, and high grazing (disturbance levels 3-5). Significantly lower species richness was found in undisturbed and lightly grazed quadrats and in ones with high soil disturbance. The change in total species richness (vascular plus non-vascular species) along the disturbance range showed a similar pattern to the vascular species richness alone; a third order polynomial regression provided the best fit (R^2= 0.27, P<0.001).

The IDH has also been supported when species abundance was added to species richness and H' represented species diversity. When H' values for vascular species alone were plotted against the disturbance gradient, a third order polynomial regression had the best fit (R^2= 0.25, P<0.001) (Figure 3-2). H' for all plant species (vascular plus non-vascular species) again showed similar results as for vascular plants alone, whereby a third order polynomial regression provided the best fit (R^2= 0.18, P<0.001). Relatively high H' values of species at the high levels of disturbance have been shown for both tested data sets.

A third order polynomial regression provided the best fit for the relationship between the evenness of vascular plants and disturbance levels (R^2 = 0.29, P<0.001) (Figure 3-3). Similar results with somewhat lower coefficient of determination were obtained for the data set which included non-vascular plants as well (R^2 = 0.20, P<0.001). Evenness showed a similar pattern of relatively high values at high disturbance levels to that observed for H'.

Diversity number N1 for each quadrat plotted against disturbance gradient had a somewhat lower fit of a polynomial regression when compared to the previous analyses. In both cases, for vascular species alone and for all plant species, a third order

polynomial regression provided the best fit (R^2= 0.19, P<0.001, and R^2 = 0.15, P<0.001, respectively).

Significant improvement of the relationship between species diversity and the disturbance gradient was achieved when H'-corrected was used as a measure of species diversity. A third order polynomial regression provided the best fit for the vascular species data set alone (Figure 3-4) as well as for one with all plant species (R^2= 0.37, P<0.001 and R^2=0.35, P<0.001, respectively). In all foregoing analyses, the addition of the third order variable was significant at P< 0.001.

Exotic species richness showed positive linear relationships only with the disturbance levels (R^2=0.12, P<0.001) (Figure 3-5). Linear relationship between exotic to native species ratio and disturbance levels had the best fit (R^2 = 0.22, P< 0.001) (Figure 3-6).

Discussion

As predicted by the IDH, significantly higher vascular plant species diversity occurred at intermediate levels of disturbance compared to levels with low or no disturbance, regardless of the measure of species diversity used. Similarly, all tests showed significant decreases of vascular species diversity at high compared to medium levels of disturbance (Figures 3-1 to 3-4). Low species richness in undisturbed and lightly grazed quadrats and the high abundance of the late succession species *Festuca hallii* (a "competitor", *sensu* Grime 1979) resulted in low species diversity (see Chapter 2 for the description of quadrat Group A from undisturbed and lightly grazed areas). These results were also consistent with the "centrifugal organization model" that predicts low species diversity in relatively undisturbed habitats occupied by the best competitor and signifficantly higher species diversity in habitats where disturbances in combination with environmental conditions prevent a strong competitor from becoming completely dominant (see discussion in the Chapter 2).

However, the high species diversity observed at high levels of disturbance in the case of H' must be explained. H' increases both with the increase of species richness and

evenness (Shannon and Weaver 1963). Results from this study showed a similar (low) species richness at low and high disturbance levels (Figure 3-1), but evenness was substantially higher at high disturbance levels than at low ones (Figure 3-3). At high levels of disturbance, physical removal of both above- and below-ground plant biomass generally prevents all species from achieving a high percent cover and dominance of others (Grime 1979). Therefore, I speculate that the unexpectedly high species diversity (H') at the highest levels of disturbance resulted from the high evenness of a relatively small number of species, none of which covered a large area of the quadrats. Results from tests of the IDH with the H'-corrected further support that speculation. The addition of exposed mineral soil as a "pseudo-species" acted like the competitive dominant *Festuca hallii* from undisturbed and lightly grazed quadrats and resulted in low species diversity at high disturbance levels.

The IDH has also been supported by the results obtained for total species diversity (vascular and non-vascular plants), regardless of the measure of diversity used. Since non-vascular species represented one fifth of the total plant species collected, results indicate that non-vascular plants may show an increase at some intermediate disturbance level similar to that of vascular species alone. However, lower coefficients of determination for H' and E obtained for total species diversity when compared to vascular species alone suggest that the evenness of non-vascular plant species may not follow closely the pattern of vascular species alone. There are two explanations for this. Firstly, a lower accuracy of percent cover estimation for non-vascular plants may result in a higher percentage of the unexplained variability. Secondly, because of their small size, non-vascular plants may have been more strongly influenced by microhabitat differences within the 1 m^2 quadrats compared to larger vascular plants. Therefore, competition between non-vascular plants with regard to different resources may occur at a smaller scale and may not be detected with the method used in my study. Future studies should consider testing the IDH for non-vascular species alone at different scales to determine whether or not there is a significant difference in the pattern of the diversity between vascular and non-vascular plant species.

Although limited, published data suggest that disturbance can have a positive influence on non-vascular species diversity. Watson (1960) and Wells et al. (1976) studied moss and lichen species in chalk grasslands in England that were grazed intensively by rabbits prior to the outbreak of myxomatosis in 1954. The authors reported significant decreases in both moss and lichen species diversity as a result of absence from selective grazing by rabbits who reduced the competitive impact of vascular plant species. Moss and lichen species in Dutch chalk grasslands suffered the same fate when land became protected from grazing by sheep. Not only did selective grazing by sheep keep the vascular herb layer low, but the fine-scale pattern of hoof prints also provided micro-habitats for numerous moss and lichen species not found in ungrazed areas (During and Willems 1986). On the other hand, studies from two national parks in eastern Canada showed that heavily disturbed habitats, such as roadside ditches, trails, parking lots, and areas around buildings, had a lower non-vascular species diversity compared to relatively undisturbed habitats (Belland and Brassard 1988, Belland and Schofield 1994).

Consistency of results with other studies

The results from my study were consistent with results from a number of other studies that supported the IDH for vascular flora in grassland communities. However, results from those studies cannot be directly compared to my results because they documented only single factors (grazing, fire, or animal burrowing) with a substantially lower range of disturbance levels, or used the time interval since the last disturbance rather than the disturbance magnitude to test the hypothesis. In Colorado's short-grass steppe, Okuda et al. (1994) found that light grazing by cattle caused higher species diversity (H') of all vascular plants and of forbs alone, compared to heavy grazing or no grazing at all; their results were consistent for all three hill-slope positions tested (upper, mid, and lower). Similarly, McIntyre and Lavorel (1994) reported the highest vascular species richness at the intermediate grazing intensity. Both species richness and diversity (N2) in an old-field plant community in Virginia were greater at a medium grazing intensity by herbivorous mammals than in undisturbed controls and more intensively grazed areas (Bowers 1993). Numerous examples of the impact of grazing on plant species diversity

from European grasslands (Huenneka 1992) and North American prairies (Collins and Glenn 1988) have suggested that grazing generally increases species diversity.

Guo (1996) studied kangaroo rats' mounds in Arizona and found that moderately disturbed areas immediately adjacent to this disturbance had significantly higher species richness then the areas on active mound and inter-mound areas. Gopher mounds of intermediate age in short-grass North American prairie had the highest species diversity (Martinsen et al. 1990). Richness of species in North American tall-grass prairies reached its maximum at an intermediate time-interval since the last fire (Collins et al. 1995). Fox (1981) tested the IDH on soil frost disturbances in alpine tundra vegetation and found maximal increase of both species richness and species diversity (N2) at intermediate levels of soil disturbances. The Intermediate Disturbance Hypothesis was confirmed even by computer simulation models such as those tested by Moloney and Levin (1996) who found that the species diversity increases at intermediate levels of disturbance.

Inconsistency of results with other studies

The Intermediate Disturbance Hypothesis was not supported in a number of studies from grassland communities. Fire is one of the most extensively tested disturbance factors in grassland vegetation. Collins *et al.* (1995) found an inverse relationship between species richness and fire frequency in tall-grass North American prairies. Collins and Glenn (1988) reviewed the effects of fire and grazing and their interaction on the diversity in North American prairies and found that species richness increased with an increase in disturbance; diversity (H') was lowest at plots only burned, and highest at burned and grazed plots. The authors concluded that the Intermediate Disturbance model inadequately represents natural dynamics in North American grasslands and that some other model should be developed that incorporates interactions of different factors. Biondini et al. (1989) investigated the timing of fire in the Northern Mixed Prairie of the USA and found that spring and fall burns resulted in lower diversity of forbs than summer burns or no burns. They suggested that under the IDH model, summer burns and the absence of fires represent disturbances to that forb community.

There are strong indications that the inconsistency of the foregoing results with results from this study reflected difference in disturbance types examined (fire vs. grazing and soil disturbances) and different climatic conditions characterizing study areas. Belsky (1992) investigated separately the effects of grazing, soil physical disturbance, fire, and competition on plant species diversity in short, mid, and tall grasslands in Tanzania. The author found that physical disturbance and protection from grazing had greater impact on species diversity than fire or the removal of dominant species. Other studies showed that fire may enhance the competitive ability of some species, such as *Agropyron gerardii* Vitman, the dominant grass in North American tall-grass prairie (Collins and Glenn 1988), *Schizachyrium scoparium*, a dominant from the North American mixed-grass prairie (Collins et al. 1995), and *Brachypodium pinnatum* (L.) Beauv., a tall, clonal graminoid from European limestone grasslands (Ryser et al. 1995). In all three cases, fire enhanced the competitive exclusion of more numerous but less competitive species, thus significantly lowering the overall species diversity. Similarly, a review of numerous studies in grasslands throughout North America suggested that the effect of fire on grassland vegetation may depend on general moisture conditions and history of the disturbance (Loucks et al. 1985). In many mesic prairies that evolved with fire (e.g., tall-grass prairie), the latter can be viewed as a large-scale phenomenon, rather than disturbance, with no measurable effect on plant species composition. However, in dry grasslands, on sandy soils, fires can weaken some of the late successional dominants and allow colonization by less competitive opportunistic species (Loucks et al. 1985). I did not investigate the effect of fire on the diversity in fescue grasslands, but Anderson and Bailey (1980) reported that annual burning significantly increased vascular species richness in undisturbed fescue grasslands near Kinsella, Alberta. In addition, Weaver and Rowland (1952) reported significantly lower species diversity in almost pure stands of *Andropogon gerardi* under long-term protection from disturbance compared to adjacent grazed areas, near Lincoln, Nebraska. Therefore, there are strong indications that both grasslands dominated by warm-season grasses, such as tall-grass prairie, and those dominated by C_3 grasses, such as fescue grasslands, may respond similarly to one type of disturbance (grazing), but oppositely to another (fire).

Although numerous studies on small-scale disturbances supported the IDH, there are some contradictory results. Martinsen et al. (1990) tested the hypothesis on disturbance by pocket gophers in short-grass prairie vegetation. Both richness and diversity of plants increased initially, but there were no significant decreases of either richness or diversity at the highest level of disturbance. The authors offered two explanations for this phenomenon: three examined levels of disturbance did not provide an adequate range for testing of the hypothesis, or forb species collected from both medium and heavily disturbed gopher mounds possessed extreme adaptations to chronic small-scale disturbances. Platt (1975) investigated species composition and diversity on and off mid-successional badgers' disturbances in North American virgin tall-grass prairie and "undisturbed", but historically overgrazed, pasture dominated by *Poa pratensis*. The author found that plots on badgers' mounds in virgin prairie supported equally high species diversity as off-mound plots (although they consisted of different sets of species), while plots on badgers' mounds in overgrazed prairie showed much higher species diversity than the off-mound plots. The latter study showed how direction of change in the plant species diversity caused by small-scale soil disturbances may be directly influenced by the definition of the undisturbed area.

Finally, it should be noted that preceding studies investigated different aspects of disturbance (frequency, magnitude, timing), which makes the interpretation and comparison of the results difficult. In addition, the size of the disturbed patches also varied considerably from study to study; therefore the scale at which the diversity of species was investigated may have influenced the results, as well.

The application for the general conceptual model of IDH

Despite the relatively high unexplained variability in my data sets (ca. 70%), my results show that the IDH holds for the within-patch (α) diversity tested on 490 1 m^2 sampling quadrats from 11 spatially separated remnants. Therefore, the present study supports the hypothesis for small-scale, within-patch diversity in grassland communities.

However, the validity of the Intermediate Disturbance Hypothesis has been vigorously debated for both aquatic and terrestrial ecosystems. Juhász-Nagu (1993) concluded that phytoplankton communities did not adequately support the IDH. He claimed that *conceptual* (e.g., scheme flora→vegetation can not be represented adequately in zoology or hydrobiology) and *methodological* (how do we measure diversity) weaknesses of the IDH model resulted in its *theoretical* weakness ("too weak to be proved or disproved"), and suggested that more attributes, such as compositional diversity and spatial-temporal coordinates, should be taken into account to move "toward a more testable hypothesis". More recent papers also suggested that a lack of clear methodological recipes for what to measure and at which scale made the IDH untestable in any given ecosystem (Bartha et al. 1997). The authors proposed a new "scale-sensitive pattern-analytical method" as a widely applicable operational definition for the IDH. However, although admitting some weaknesses of the IDH, such as difficulties in the recognition and measurement of the disturbance, Reynolds *et al.* (1993) suggested that these difficulties do not discredit the IDH. The authors justified the adaptation of the IDH in phytoplankton ecology because of its comprehensiveness and simplicity, and its applicability in general ecology and in the management of ecosystems. It is now up to future studies in different ecosystems to show if the recent attempts to bring the IDH from a "general conceptual framework" to the "testable hypothesis" will result in a higher consistency between results obtained for different habitats studied (grasslands, forests, aquatic systems).

Unexplained variability in the data set with vascular species alone

Results from data sets for vascular species alone suggest that the magnitude of the disturbance (independent variable) may be related to an ecological factor governing species diversity; however, species diversity is also influenced by some other factors responsible for the unexplained variability in the species data set. It should be noted that the high dependence of the species diversity on a disturbance regime may often result from situations where quantification of the biotic response, rather than the quantification of stimulus, leads to circular reasoning (Sommer et al. 1993). In such a case, the strength of the disturbance is the strength of the biotic response. By grouping observed disturbances objectively into ten categories with no reference to the vegetation

appearance, and, subsequently, creating a disturbance ranking by ordering these categories based on the percentage of exposed mineral soil, I avoided circular reasoning. However, this objectivity may be partially responsible for the somewhat lower predictability of the diversity pattern at different levels of the disturbance (from $R^2 = 0.23$ for S up to $R^2 = 0.37$ for H'-corrected).

Sommer et al. (1993) indicated that researchers experience significant problems when analizing survey data because only in experimental studies all factors other than those to be tested can be held constant. A number of factors, such as the time since the last disturbance and disturbance frequency, have not been controlled in my study (with the exception of two time-intervals for soil mixing) and may account for part of the unexplained variability in the data set. As originally proposed (see Connell 1978) and often tested (e.g. Collins et al. 1995), richness and diversity of species are generally highest at some intermediate disturbance magnitude, frequency, and intermediate time interval since the last disturbance. Guo (1996) studied plant species diversity on kangaroo rat mounds and found great variation in diversity on active mounds as a result of different disturbance frequencies, and in inactive ones because they represented different stages of succession. In the present study, I split quadrats with soil-mixing into two time periods (up to two years and more than two years since the last disturbance). This resulted in a significant difference in the average percentage of exposed mineral soil and in the species richness and diversity between the two groups. Consequently, recently disturbed quadrats (most of them were still active animal mounds) moved toward the highest disturbance levels, while old ones were placed between medium and high grazing disturbance levels. Higher species richness and diversity of the older disturbances when compared to the recent ones was probably due to the advanced succession of the first one. In addition, one old pipe-line and old animal mounds in this level of disturbance were sampled in areas that were ungrazed for a number of years, thus resulting in a faster succession. Platt (1975) reported a very similar species diversity and equitability on and off old disturbance patches in virgin prairie, although there was a difference in species composition even 20 years after the disturbance. A separation of other disturbance groups in my study based on disturbance frequency and time since the last disturbance was not

possible because of limited historical information (e.g., frequency of cow path use or time since the last use of bison wallow), but may have given different results.

Although grassland remnants within the aspen parkland can be classified generally as fescue grasslands, the influence of regional differences in climate, topography, and soils, as well as possible historical differences in management of 11 spatially separated remnants, have most likely resulted in a different species composition within each of the grasslands studied. Local environmental factors, such as soil moisture, texture, or fertility (Sousa 1984, Nilsson *et al* 1989, Tilman and Downing 1994, Tilman 1996), and regional climatic differences (see discussion in Chapter 2), are often responsible for the variability in plant species composition. Austin and Smith (1989) warned that investigations of the plant species response to disturbance regime should not ignore underlying environmental factors, such as resources (light, nutrients, water) and direct factors (soil pH or temperature). Bartha et al. (1995) also suggested that the interaction between these large- and small-scale environmental influences produces a complex pattern of vegetation along a range of spatial and temporal scales. Moreover, they argued that disturbance, such as grazing, cause a high stochastic variability of species distribution and abundance at the small-scale. They explained the phenomenon by a large number of species belonging to only a few functional groups, so that their combinations resemble random expectations. Bartha et al. (1995) also investigated the influence of slope position on species richness and diversity and their associations in North American tall-grass prairie. Not only did they find a significant increase in species richness from lowland toward hilltop, they also found a similar pattern of increase in the spatial dependence among species. When viewed from the perspective of my study, Bartha *et al.* (1995) suggest that the local differences in the community species pool may influence directly the number of species available for the invasion of "competition free" spaces resulting from small-scale disturbances. In addition, Huston (1979) suggested that the growth rate of each species within a given community is as important as disturbance for species diversity. The growth rate of a single species differs widely in nature depending on local conditions. Adapted species may increase the growth rates with increased rates of disturbances, resulting in an unexpectedly high species diversity (Huston 1979).

Diversity of exotic species

The present study confirmed the prediction of the second hypothesis that the richness of exotic vascular plants will show a positive relationship with disturbance levels. The dense carpet of live *Festuca hallii* and its standing litter that covers undisturbed and lightly grazed areas in remnant grasslands (Chapter 2) left little space for the successful establishment of other species, including exotic ones. The significant increase of exotic species richness with increased magnitude of the disturbance reflected the decrease of shade by fescue and its litter, as well as the increase in available exposed mineral soil required by exotic species (mostly "ruderals", *sensu* Grime 1979) at least for initial establishment. Lastly, high soil disturbances were well suited for exotic species and resulted in their higher richness compared to soils with medium disturbances.

The third hypothesis that predicted that exotic vascular plant species will be mainly responsible for a disproportionate amount of the total vascular species diversity at the intermediate disturbance levels was not supported. Although ratios of exotic to native species showed a significant positive linear relationship with the disturbance levels (Figure 3-6), the "hump" representing total vascular species richness at intermediate disturbance levels (Figure 3-1) indicates that native species richness predominated over exotic species richness. There are at least two explanations for these results. Firstly, native species represented the majority (85%) of the total number of vascular plant species collected. Therefore, it is reasonable to assume that they will contribute predominantly to the species diversity in quadrats without heavy soil disturbances that support a large number of different species. Secondly, my results may have reflected pre-adaptations of native and exotic taxa to different environments. On a large time-scale, vegetation of native fescue grasslands in south-central Alberta have experienced relatively predictable large-scale disturbances, such as natural and "Indian-caused" fires, and seasonal grazing by large, hoofed animals, such as bison and, to some degree, prong-horned antelope (*Antilocapra americana* Ord.), with no agriculture practices prior to the European settlement (Bird 1930, 1961, Rowe and Coupland 1984). Although temporal and spatial distribution of bison is still highly speculative, there are numerous references to its historical association with the aspen parkland (Fidler 1990, Campbell 1994). The

importance of historical evolvement of temperate grasslands from the Great Plains, including fescue grasslands with bison, has been discussed extensively by Mack (1989). The author speculated that higher resilience of native grasslands from the North Plains of North America to invasion by exotic species compared with Californian and some other North American and Australian grasslands, resulted from strong evolutionary selection toward native rhizomatous and caespitose grasses tolerant of periodic disturbances by bison.

Soils that support grassland vegetation in the aspen parkland area range from fertile Black Chernozem Soils to soils generally low in fertility, such as sandy Regosols, and Dark Brown Soils. In addition, regional climatic conditions, especially available moisture during the growing season, show a gradient from relatively dry conditions in the southeastern portion of the aspen parkland to relatively moist conditions toward the northwest portion of the region (Figure 1-2, Chapter 2). This resulted in a possible preadaptation of native grassland species in the aspen parkland of Alberta to different soil and climatic conditions but not to heavy soil disturbance. Fox and Fox (1986) suggested that the interactions of native species through evolutionary and ecological times generally result in an inter-connected framework of species preadapted to prevailing environmental conditions. In support of this theory, my ordination analysis (Chapter 2) showed a large number of native species preadapted to stressful conditions, such as increased soil sodicity or inadequate moisture ("stress tolerants", *sensu* Grime 1979). In addition, I also found a relatively large number of native fugitive species (mostly "ruderals", *sensu* Grime 1979) that are known to grow in disturbed areas, such as roadsides, waste grounds, and soil erosions (Chapter 2).

In contrast to native taxa, most of the exotic species that accompanied European settlement from its earliest days are adapted to well-watered, fertile soils and to disturbances resulting from urbanization and intensive agricultural practices (heavy grazing and cultivation) (Mack 1986). In Australian grasslands, with historical conditions similar to Alberta's grasslands, McIntyre and Lavorel (1994) separately studied exotic species richness in relation to two anthropogenic water enrichment levels, three levels of

grazing, and three levels of soil disturbances. Although no significant effect of grazing levels upon the exotic species richness was apparent, they did find a consistent increase of exotic species richness with an increase in soil disturbances and water enrichment. Negative responses of exotic species in my study to a lack of available moisture (a result of dry climatic conditions, coarse soil texture, or from high solar radiation on south and southeast facing slopes) have been discussed and related to results from other studies in Chapter 2.

Huenneke et al. (1990) found that the addition of nutrients to otherwise nutrient-poor serpentine soils enhanced exotic species invasion and the replacement of native serpentine species from native Californian grasslands. In their field experiments on plant competition and resource availability in Minnesota, Wilson and Tilman (1993) found a significant increase in growth rates of *Poa pratensis* and *Agropyron repens* with the addition of nitrogen, while no such response was found in the native species *Schizachyrium scoparium*. The authors suggested that *S. scoparium* may exhibit a relatively high nitrogen use efficiency when compared with the other two species. In my study (Chapter 2), the highest abundance of *P. pratensis* and *Taraxacum officinale* corresponded to relatively high soil nitrogen content. Finally, the majority of exotic species require disturbance-mediated open spaces at least for their initial establishment (Mooney and Drake 1986). The majority of exotic species in my study showed a high positive correlation with exposed mineral soil resulting from disturbances (Chapter 2).

Therefore, the relatively low diversity of exotic species at intermediate and high levels of disturbance may be attributed to stressful environmental conditions, such as high sodicity or lack of adequate moisture. Over the wide range of climatic and soil conditions that characterize the 11 remnants that I sampled, combinations of different stressful conditions, to which the native flora is pre-adapted, and the relatively small size of the disturbances may have prevented the successful establishment of exotic species. Hobbs (1989) and Hobbs and Huenneke (1992) suggested that in the absence of increased nutrient availability, higher soil disturbances do not necessarily result in exotic species invasion.

Relatively few studies have investigated the diversity of exotic species in relation to disturbance. In their study of two riparian plant communities from southwest France and Oregon, Planty-Tabacchi et al. (1995) found the highest exotic species richness at the intermediate disturbance levels coinciding with the highest total species richness. In contrast to my study, exotic species represented ca. 30% of the total flora. Pyle (1995) studied exotic species invasion of the river floodplain in Maryland and found that anthropogenic disturbances due to recreational use and deforestation of the area resulted in significantly greater exotic species invasion than in the naturally flooded adjacent areas. The authors suggested that exotic species responded more positively to anthropogenic than to natural disturbances, such as those by regular frequent flooding. In contrast, DeFerrari and Naiman (1994), who conducted a similar study on the Olympic Peninsula, Washington, found a significantly higher number of exotic species in riparian zones than adjacent clearcuts. They argued that frequent flooding represented a high disturbance level supporting an exotic species invasion, while deforestation often leaves a relatively intact understorey of native plants.

Applications for the management of grassland communities

The importance of maintaining a high diversity of plant species has been the center of attention in numerous studies of fundamental ecology and conservation issues. Tilman and Downing (1994) found that species-rich plots resulted in better ecosystem resistance to drought, because they were more likely to have some drought-resistant species. In addition, higher species diversity resulted in better use of soil nitrates that are important in nutrient cycling processes (Tilman et al. 1996). As postulated by the IDH and confirmed through numerous studies, including this one, disturbance plays a significant role in the coexistence of a large number of plant species, both at the small-scale and the community levels. Although I explicitly tested the IDH for within-patch (α) diversity at a small-scale (as originally proposed by Connell 1978), my preliminary survey of 120 prairie remnants in the Aspen Parkland of Alberta showed a high habitat homogeneity in the absence of cattle grazing in areas protected for wildlife management (Vujnovic and Wein 1997). In the dense "carpet" of the dominant prairie grass *Festuca hallii* that covers

acres of unbroken land, gaps, such as frequently used cow paths or recent burrows from Richardson ground squirrels', were absent. These kinds of small-scale disturbances are known to be positively related to grazing by cattle or bison (Bird 1961). Thus, I speculate that different cattle grazing intensities and other small-scale disturbances that accompany grazing within my study area provided a habitat heterogeneity that most likely resulted in higher between-patches (β) diversity than the diversity of protected, undisturbed grasslands.

Generally, gaps of exposed mineral soil resulting from disturbances represent "temporary windows" (*sensu* Johnstone 1986) for invasion of a number of new fugitive species. However, exotic species often represent a significant proportion of the species diversity on highly disturbed habitats. As they have evolved with the anthropogenic disturbances, such as plowing and pasture overgrazing by cattle, exotic species are often opportunistic and exhibit phenotypic plasticity in order to sustain unpredictable changes in the environment (Groves and Burdon 1986, Mooney and Drake 1986). Once established, exotic invaders may alter the environment by being nitrogen fixers or by bringing salts to the surface, hence, altering the direction of succession (Baker 1986, Bazzaz 1986). Although there may be a good source of native species preadapted to small-scale disturbances, the disturbed grassland gaps also represent a window for potentially invasive exotic species if they become introduced in the future. As it has already been recognized by Fox and Fox (1986), Hobbs and Huenneke (1992), and McIntyre and Lavorel (1994), when considering the management of conservation areas, a balance should be made between disturbances required for maintenance of high native species diversity and that which may result in invasion of exotic species. Therefore, a relatively high H' for significantly disturbed quadrats with small vegetation cover, such as these shown in my study, has to be taken with caution. I suggest that when the diversity of plant species in grassland communities is being measured for conservation purposes, Shannon's Diversity Index corrected for the exposed mineral soil should be considered. Therefore, management practices that result in high species diversity in habitats with a relatively low percentage of exposed mineral soil (an indicator of disturbance level) should be encouraged.

Scientific Contribution

This is the first study to focus on the relationships between small-scale disturbances and plant species diversity in the fescue grasslands. Inclusion of non-vascular species in the test of the Intermediate Disturbance Hypothesis for the grassland community is also unique. This is also one of the few studies that related exotic species richness to different levels of disturbance. Finally, this study proposes a correction for the diversity index (H'-corrected), which may prove useful in future assessments of the quality of native grasslands in regards to the species diversity.

Conclusions

The IDH has been supported for small-scale within-patch diversity regardless of the measure of diversity used. Low species diversity in undisturbed and lightly grazed quadrats resulted from the dominance of a competitive species of virgin prairie, *Festuca hallii*. High levels of disturbance that remove most of the vegetation and significantly change soil physical and chemical properties supported low species diversity. Intermediate levels of disturbance (medium and heavy grazing, old soil mixing) that lowered the competitive ability of *F. hallii* supported the highest species diversity. Similar results were obtained for both the total number of plant species (non-vascular plants included) and the number of vascular plant species alone. Exotic vascular species showed a significant but weak positive relationship with the magnitude of the disturbance. The prediction that exotic vascular plant species will account for a disproportionate amount of the total vascular species diversity at intermediate disturbance levels was not supported.

Table 3-1. Order of ten levels of disturbance as used to relate plant species diversity to the magnitude of disturbance. Order in the first column have been subjectively chosen based on the type of disturbance sampled. The second column has been derived after calculating mean % exposed mineral soil for each type of disturbance and arranging types of disturbance in ascending order of the % exposed mineral soil.

	Order before adjustment for % exposed mineral soil	Order after adjustment for % exposed mineral soil
1	no vegetation or soil disturbance	no vegetation or soil disturbance
2	light grazing with no soil disturbance	light grazing with no soil disturbance
3	moderate grazing with soil compaction	moderate grazing with soil compaction
4	heavy grazing with soil compaction	more than two-years-old mixing of soil
5	vehicle or cow paths with soil compaction	heavy grazing with soil compaction
6	more than two-years-old mixing of soil	vehicle or cow paths with soil compaction
7	up to two-years-old mixing of soil	removal of up to 10 cm of soil
8	removal of up to 10 cm of soil	removal of more than 50 cm of soil
9	removal of 10-30 cm of soil	up to two-years-old mixing of soil
10	removal of more than 50 cm of soil	removal of 10-30 cm of soil

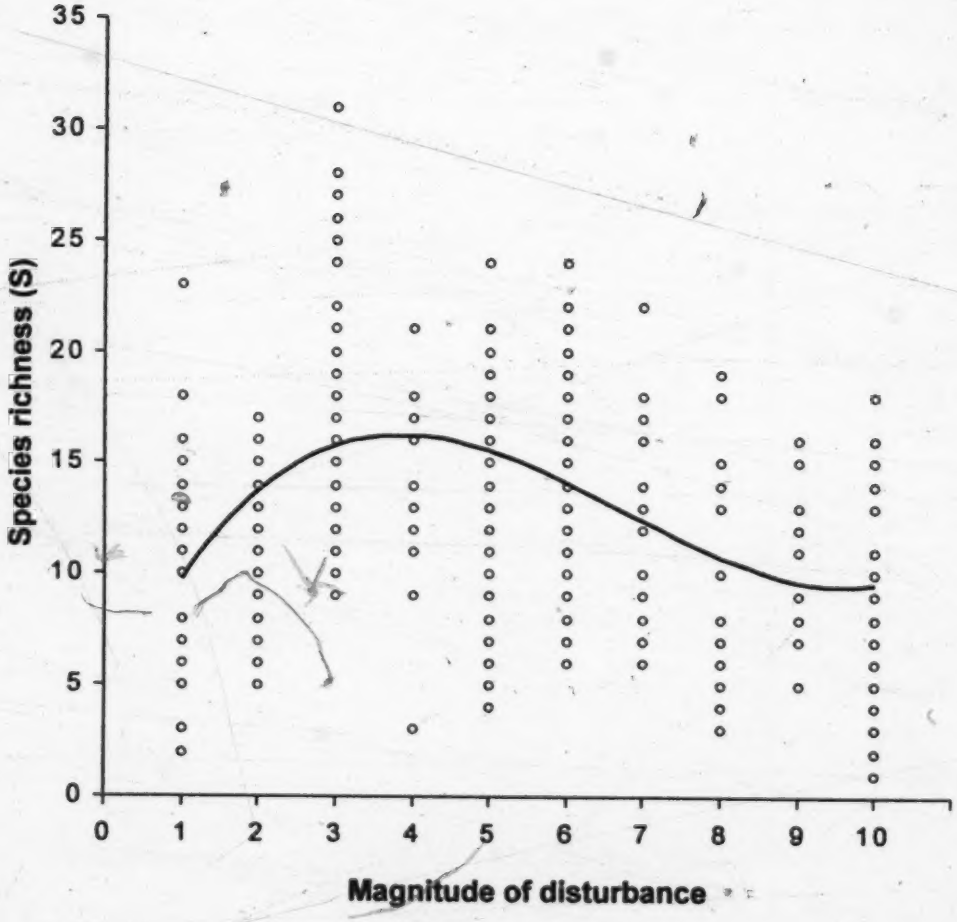

Figure 3-1. The relationship between vascular plant species richness (S) and magnitude of the disturbance at 490 1 m^2 quadrats from remnant grasslands in the aspen parkland ($N = 490$; $y = 0.0697\ x^3 - 1.4094\ x^2 + 7.7352\ x + 3.3778$; $R^2 = 0.23$; $p < 0.001$).

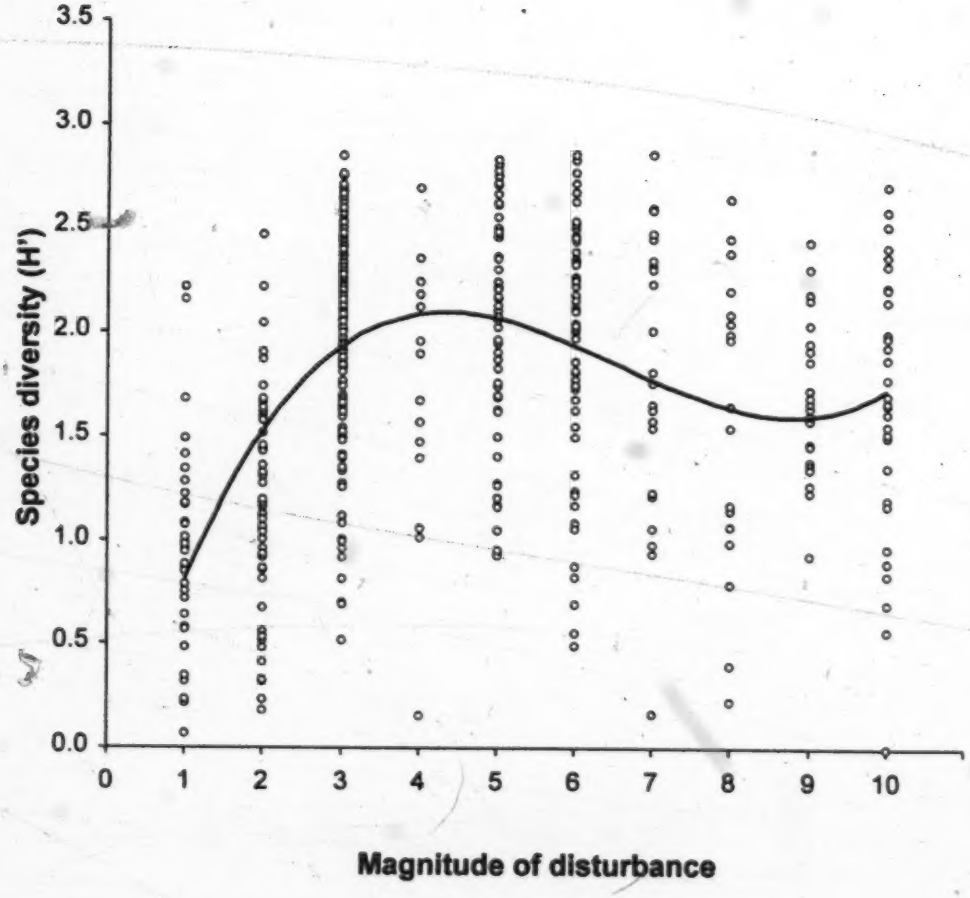

Figure 3-2. The relationship between vascular plant species diversity (H') and magnitude of the disturbance at 490 1 m^2 quadrats from remnant grasslands in the aspen parkland ($N = 490$; $y = 0.0114 x^3 - 0.2241 x^2 + 1.3045 x + 0.2735$; $R^2 = 0.25$; $p < 0.001$).

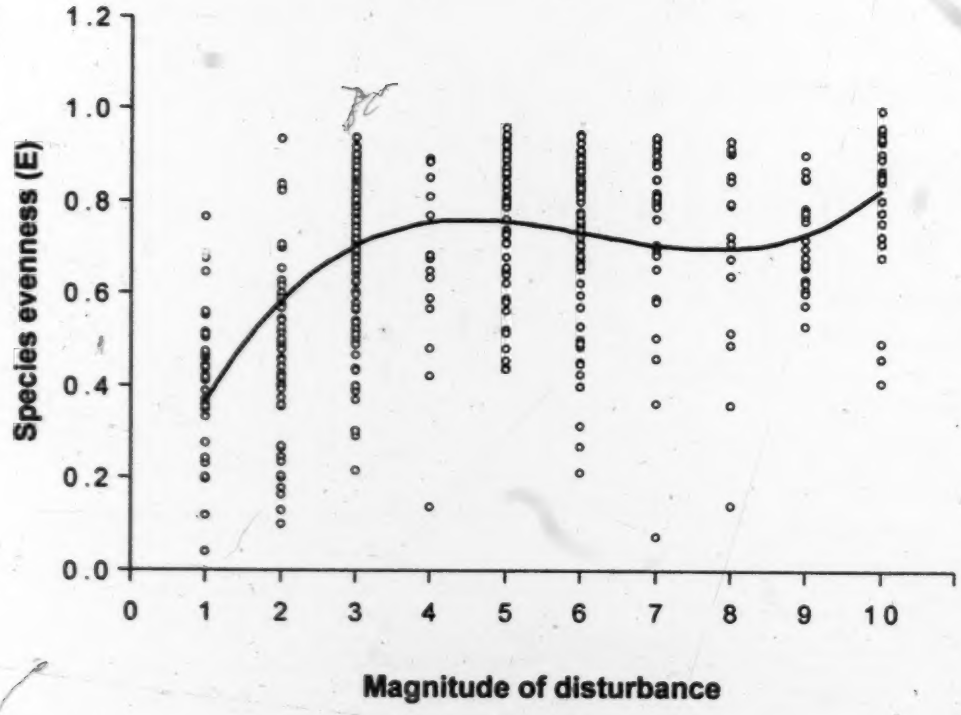

Figure 3-3. The relationship between evenness of vascular plant species (E) and magnitude of the disturbance at 490 1 m^2 quadrats from remnant grasslands in the aspen parkland (N = 490; $y = 0.0037 x^3 - 0.0687 x^2 + 0.3945 x + 0.0374$; $R^2 = 0.29$; $p < 0.001$).

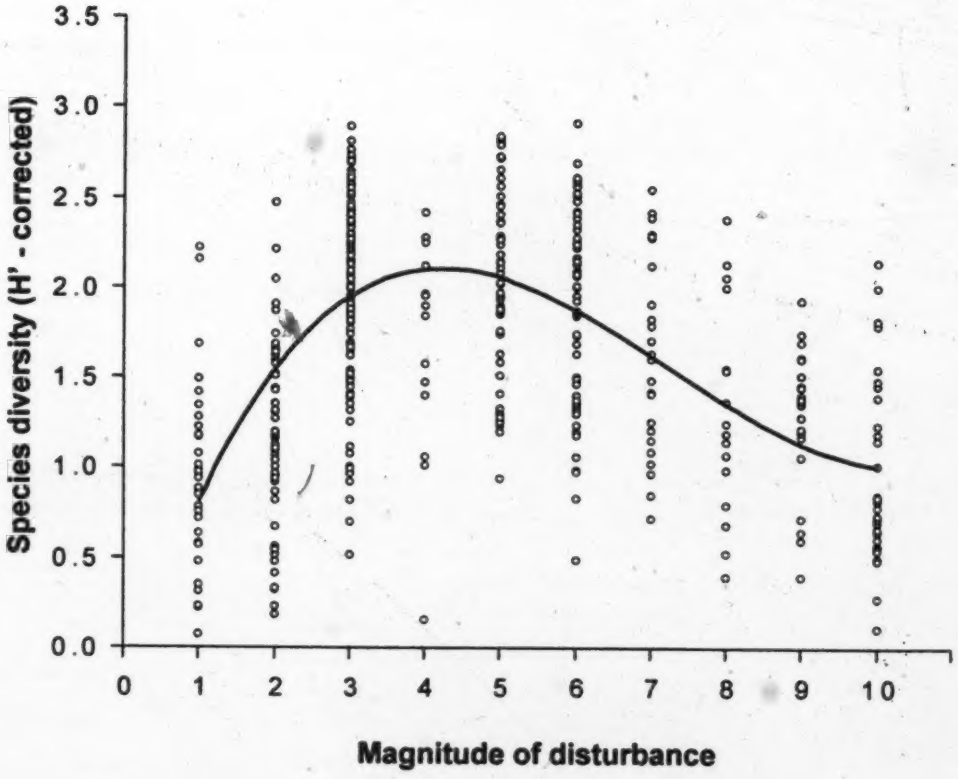

Figure 3-4. The relationship between vascular plant species diversity (H' - corrected) and magnitude of the disturbance at 490 1 m^2 quadrats from remnant grasslands in the aspen parkland (N = 490; $y = 0.0101 x^3 - 0.2194 x^2 + 1.3129 x + 0.2931$; $R^2 = 0.37$; $p < 0.001$).

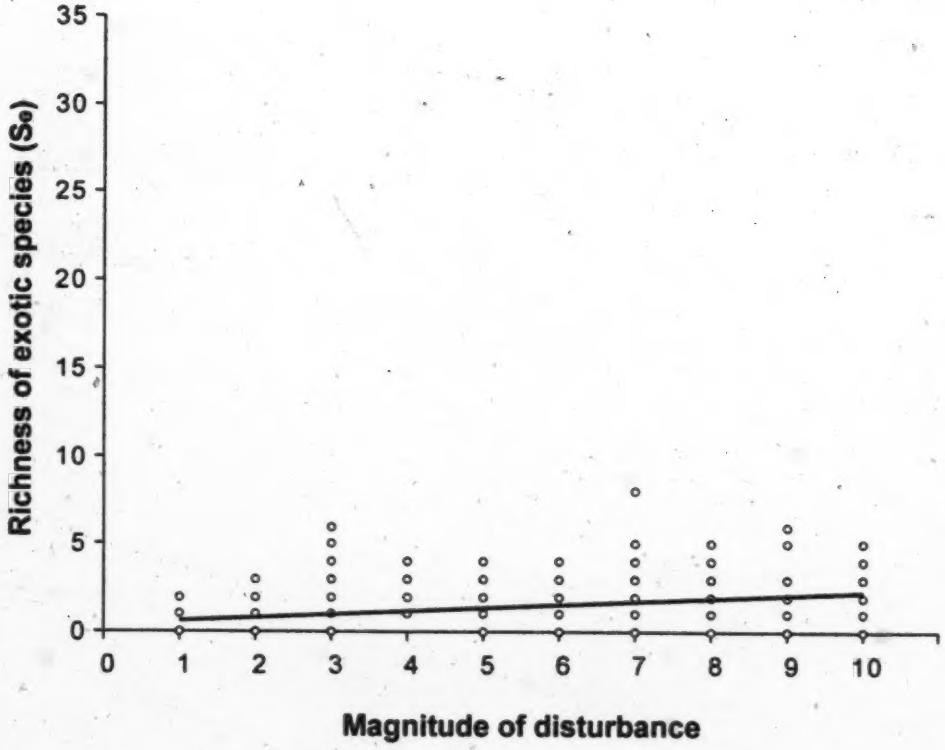

Figure 3-5. The relationship between richness of exotic vascular plant species (S_e) and magnitude of the disturbance at 490 1 m^2 quadrats from remnant grasslands in the aspen parkland ($N = 490$; $y = 0.1833\ x + 0.4653$; $R^2 = 0.12$; $p < 0.001$).

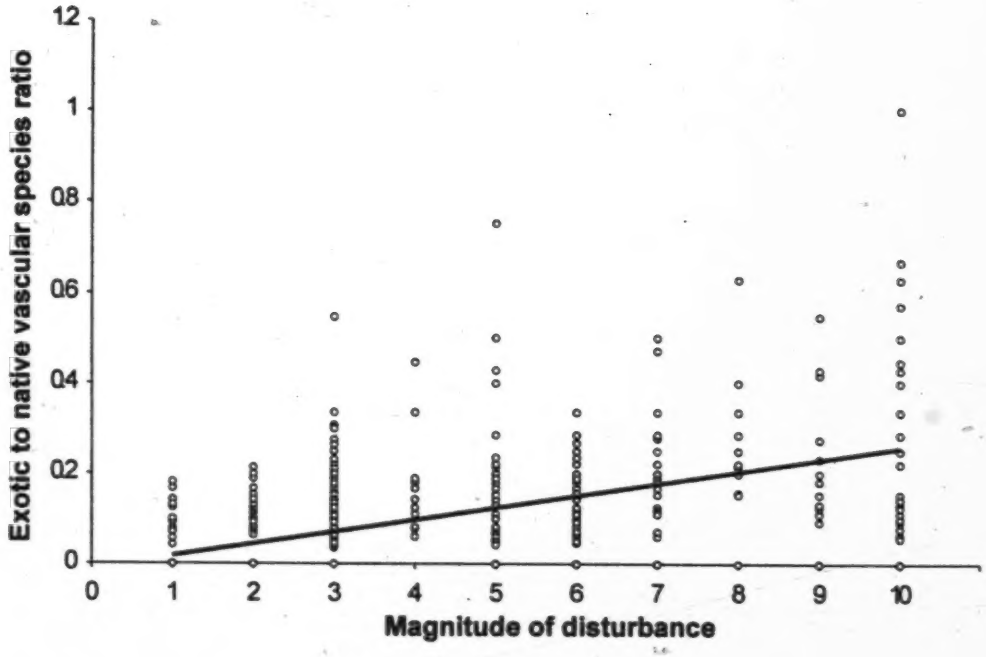

Figure 3-6. The relationship between exotic to native plant species ratio and magnitude of the disturbance at 490 1 m^2 quadrats from remnant grasslands in the aspen parkland ($N = 490$; $y = 0.0266 x + 0.0081$; $R^2 = 0.22$; $p < 0.001$).

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CHAPTER 4
CONCLUSIONS

Examination of 11 remnant areas of native grassland within the aspen parkland of Alberta revealed a high number of native vascular plant species (174) and a significantly lower number of exotic ones (31). This study showed the important role of small-scale vegetation and soil disturbances in shaping plant species composition and diversity. Specific conclusions, which refer to the five objectives listed in the Chapter 1, include:

1. The complexity of habitat characteristics underlying small-scale plant species composition in the fescue grasslands of the aspen parkland is reflected in the high number of quadrat groups (19) derived by cluster analysis. The largest quadrat group, containing about one quarter of all quadrats, was characterized by the absence of disturbances other than light grazing and by the dominance of *Festuca hallii* to the exclusion of other vascular plant species. Disturbances, which result in the removal of standing litter and live cover of *Festuca hallii*, allowed other plant species to invade, therefore showing that disturbance is the most important factor influencing small-scale plant species composition. Five environmental variables (soil nitrogen, soil clay and sand contents, soil sodicity, and annual solar radiation received by the area) and two spatial variables (latitude and longitude) revealed complex moisture and stress gradients to which plant species respond once disturbances, such as moderate grazing and soil mixing, occur. Drought-tolerant species invade drier areas (southeastern aspen parkland, south-facing slopes, or dry sandy soils), halophytes invade sodic soils, and ruderals become important components of disturbed and mesic areas.

2. The majority of exotic species showed a clear preference for disturbed, moist habitats, largely coinciding with geographical position within the northwestern portion of the aspen parkland of Alberta. This indicates the equal importance of environmental conditions (ample moisture) and disturbance (pre-empted space) for exotic species invasion into fescue grasslands. Two exceptions were the drought-tolerant competitors, *Agropyron pectiniforme* and *Bromus inermis* ssp. *inermis*, which were found in disturbed

dry areas, indicating that these species may invade regardless of moisture conditions. *Poa pratensis* was associated with moist soils and high levels of soil mineral nitrogen.

3. Small-scale vascular plant species composition in the fescue grasslands follows the "centrifugal organization model" previously described for forest and wetland communities. A single competitor, *Festuca hallii,* dominates the relatively undisturbed (core) habitats. Once disturbance reduces the competitive dominance of *Festuca hallii,* the species pool increases. The actual resulting vascular plant species composition depends on the disturbance magnitude and environmental conditions, such as soil moisture, soil sodicity, and soil nutrient levels. The interactions between environmental conditions and disturbances result in high diversity of species assemblies that radiate out from the core habitat. In contrast to wetlands and forests, the core habitat in fescue grasslands does not have the most fertile soil.

4. The Intermediate Disturbance Hypothesis was supported for vascular plant species alone and for all plant species (non-vascular species included) regardless of the measure of diversity used. However, the highest coefficients of determination were obtained when H'-corrected was used as a measure of species diversity. Richness of exotic vascular species showed a significant but weak positive relationship with the magnitude of the disturbance. Native species richness predominated over exotic species richness at all levels of disturbance because of a generally low proportion of exotic species and the variable response of exotic species to the disturbances under different environmental conditions, such as moisture and fertility.

5. There are a number of management implications. There is a conflict between agricultural use and conservation of remnant fescue grasslands within the aspen parkland. The majority of remaining unbroken land (including protected areas) within the aspen parkland supports the cattle industry. The aspen parkland currently supports approximately 30% of the provincial cattle production (Horton et al. 1992). On the other hand, because so few fescue grasslands are left in the Canadian Prairie Provinces (Weins 1996, Diamond 1993) there is a concern that even the smallest remnant of native

grassland in good condition should be protected from overgrazing (Anonymous 1997). Areas of relatively undisturbed lush fescue support numerous declining wildlife species, such as Baird's sparrow (*Ammodramus bairdii*), and rare plant species, such as *Viola pedatifida* G. Don. (Wershler and Wallis 1990). It is also confirmed that ungrazed fescue grasslands support a significantly higher richness of avian species compared to grazed fescue pastures (Prescott et al. 1995). Therefore, it is not surprising that Wershler and Wallis (1990) suggested that the current grazing regime over most of the fescue grasslands in Alberta conflicts with conservation goals. Finally, long-term fire suppression and exclusion of roaming herds of bison are held responsible for loss of fescue grasslands to trees and shrubs in the parkland area (Bailey and Wroe 1974, Campbell et al. 1994), thereby suggesting a positive effect of grazing and fire for the preservation of open grassland areas.

Results from the present study suggest that cattle grazing and accompanying small-scale disturbances, such as cow paths, areas of heavy grazing, and animal burrows significantly increase diversity of native plant species compared to ungrazed areas in remnant fescue grasslands. Under the present climatic conditions, protection of both moderately grazed, diverse native grasslands and relatively undisturbed lush fescue grasslands would provide grassland habitat diversity at the landscape level. Relatively undisturbed fescue grasslands also provide key wildlife habitat and source for native seed collection. However, active management, such as combination of prescribed burning and grazing, will have to be considered for these areas in order to prevent tree and shrub invasions.

Any management actions that would lead to moisture and nutrient enrichment in fescue grasslands in the aspen parkland should be avoided to prevent exotic species invasion. *Poa pratensis* already has invaded many heavily grazed pastures in Alberta to the point of complete dominance; farmers recognize these pastures as a problem because of their low productivity. No serious infestations of drought-tolerant species such as *Bromus inermis* and *Agropyron pectiniforme* were found in the present study, but both species are known to invade native grasslands; therefore, their intentional planting for reclamation purposes should be avoided.

Finally, disturbance that leads to prolonged removal of dense fescue stands and of standing litter, thereby negatively influencing spring soil moisture conditions, will enhance replacement of fescue grasslands with mixed-prairie grassland communities under global warming. Presently, this replacement can be observed on the hilltops and south-facing slopes in protected areas, which are grazed by wildlife in the spring (personal observations), and in the pastures because of cattle's preference to graze these areas (Wroe 1971 and Wheeler 1976). Until today, no long-term successful seeding of *Festuca hallii* has been reported (Walker 1992). Therefore, in case of continuous climate warming, a higher proportion of remnant fescue grasslands should be actively managed by prescribed burning and grazing only in order to preserve threatened lush fescue grasslands.

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APPENDICES

Appendix 1. Taxonomic names for vascular and non-vascular plant species and corresponding six-letter abbreviations used in tables and figures.....165

Appendix 1. Taxonomic names for vascular and non-vascular plant species and corresponding six-letter abbreviations used in tables and figures.

Scientific name	CODE
Grasses	
Agropyron albicans Scribn. & Smith	AGRALB
Agropyron dasystachyum (Hook.) Scribn.	AGRDAS
Agropyron hyb.	AGRHYB
Agropyron pectiniforme R. & S.	AGRPEC
Agropyron repens (L.) Beauv.	AGRREP
Agropyron smithii Rydb.	AGRSMI
Agropyron trachycaulum var. *trachycaulum* (Link) Malte	AGRTRA
Agropyron trachycaulum var. *unilaterale* (Cassidy) Malte	AGRUNI
Agrostis scabra Willd.	AGRSCA
Agrostis stolonifera L.	AGRSTO
Bouteloua gracilis (HBK) Lag.	BOUGRA
Bromus inermis ssp. *inermis* Leyss.	BROINE
Bromus inermis ssp. *pumpellianus* (Scribn.) Wagnon	BROPUM
Calamovilfa longifolia (Hook.) Scribn.	CALLON
Danthonia californica Boland	DANCAL
Deschampsia cespitosa (L.) Beauv.	DESCES
Distichlis stricta (Torr.) Rydb.	DISSTR
Elymus canadensis L.	ELYCAN
Festuca hallii (Vasey) Piper	FESHAL
Festuca rubra L.	FESRUB
Festuca saximontana Rydb.	FESSAX
Helictotrichon hookeri (Scribn.) Henr.	HELHOO
Hierochloe odorata (L.) Beauv.	HIEODO
Hordeum jubatum L.	HORJUB
Koeleria macrantha (Ledeb) J.A. Schultes f.	KOEMAC
Muhlenbergia cuspidata (Torr.) Rydb.	MUHCUS
Muhlenbergia richardsonis (Trin.) Rydb.	MUHRIC
Oryzopsis pungens (Torr.) A.S. Hitchc.	ORYPUN
Phleum pratense L.	PHLPRA
Poa arida Vasey	POAARI
Poa canbyi (Scribn.) Piper	POACAN
Poa compressa L.	POACOM
Poa interior Rydb.	POAINT
Poa palustris L.	POAPAL
Poa pratensis L.	POAPRA
Poa spp.	POASPP
Puccinellia nuttalliana (Schult.) A. S. Hitch.	PUCNUT
Spartina gracilis Trin.	SPAGRA
Stipa comata Trin. & Rupr.	STICOM
Stipa curtiseta (A.S.Hitchc)	STICUR
Stipa viridula Trin.	STIVIR
Sedges and Rushes	
Carex brevior (Dewey) Mack.	CARBRE
Carex douglasii Boott	CARDOU
Carex obtusata Lilj.	CAROBT
Carex pensylvanica Lam.	CARPEN

Carex praegracilis W. Boott	CARPRA
Carex praticola Rydb.	CARPRT
Carex siccata Dewey	CARSIC
Carex spp.	CARSPP
Carex stenophylla Wahl.	CARSTE
Carex xerantica Bailey	CARXER
Juncus balticus Willd.	JUNBAL
Juncus bufonius L.	JUNBUF
Juncus tenuis Willd.	JUNTEN
Juncus vaseyi Engelm.	JUNVAS

Forbs

Achillea millefolium L.	ACHMIL
Agosereis glauca (Pursh) Raf.	AGOGLA
Agrimonia striata Michx.	AGRSTR
Allium textile Nels. & Macbr.	ALLTEX
Androsace septentionalis L.	ANDSEP
Anemone cylindrica A. Gray	ANECYL
Anemone multifida Poir.	ANEMUL
Anemone patens L.	ANEPAT
Antennaria neglecta Greene	ANTNEG
Antennaria spp.	ANTSPP
Arabis divaricarpa A. Nels	ARADIV
Arabis hirsuta (L.) Scop.	ARAHIR
Arabis holboellii Hornem.	ARAHOL
Aralia nudicaulis L.	ARANUD
Arnica fulgens Pursh	ARNFUL
Artemisia biennis Willd.	ARTBIE
Artemisia campestris L.	ARTCAM
Artemisia frigida Wiolld.	ARTFRI
Artemisia ludoviciana Nutt.	ARTLUD
Aster borealis (T. & G.) Prov.	ASTBOR
Aster ericoides L.	ASTERI
Aster laevis L.	ASTLAE
Astragalus dasyglottis Fisch. *ex* DC.	ASTDAS
Astragalus drummondii Dougl.*ex* Hook	ASTDRU
Astragalus flexuosus Dougl. *ex* G. Don	ASTFLE
Astragalus gilviflorus Sheldon	ASTGIL
Astragalus striatus Nutt.	ASTSTR
Atriplex nuttallii S. Wats.	ATRNUT
Axyris amaranthoides L.	AXYAMA
Campanula rotundifolia L.	CAMROT
Capsella bursa-pastoris (L.) Medic.	CAPBUR
Cerastium arvense L.	CERARV
Chenopodium album L.	CHEALB
Cirsium arvense (L.) Scop.	CIRARV
Cirsium flodmanii (Rydb.) Arthur	CIRFLO
Collomia linearis Nutt.	COLLIN
Comandra umbellata (L.) Nutt.	COMUMB
Cornus canadensis L.	CORCAN
Crepis runcinata (James) T. & G.	CRERUN
Crepis tectorum L.	CRETEC
Descurainia sophia (L.) Webb	DESSOP
Draba nemorosa L.	DRANEM
Epilobium angustifolium L.	EPIANG

Equisetum arvense L.	EQUARV
Equisetum hyemale L.	EQUHYE
Erigeron annuus (L.) Pers.	ERIANN
Erigeron caespitosus Nutt.	ERICAE
Erigeron glabellus Nutt.	ERIGLA
Erigeron spp.	ERISPP
Fragaria virginiana Duchesne	FRAVIR
Gaillardia aristata Pursh	GAIARI
Galium boreale L.	GALBOR
Gaura coccinea Pursh	GAUCOC
Gentianella amarella (L.) Borner	GENAMA
Geum aleppicum Jacq.	GEUALE
Geum triflorum Pursh	GEUTRI
Grindelia squarrosa (Pursh) Dunal	GRISQU
Gutierrezia sarothrae (Pursh) Britt. & Rusby	GUTSAR
Hedysarum alpinum L.	HEDALP
Helianthus nuttallii L.	HELNUT
Helianthus subrhomboideus Rydb.	HELSUB
Heterotheca villosa (Pursh) Shinners	HETVIL
Heuchera richardsonii R.Br.	HEURIC
Hieracium umbellatum L.	HIEUMB
Lactuca pulchella (Pursh) DC.	LACPUL
Lappula occidentalis (S. wats.) Greene	LAPOCC
Lathyrus ochroleucus Hook	LATOCH
Lepidium densiflorum Schrad.	LEPDEN
Lesquerella arenosa (Richards.) Rydb	LESARE
Lygodesmia juncea (Pursh) D. Don	LYGJUN
Maianthemum canadense Desf.	MAICAN
Matricaria matricarioides (Les.) Porter	MATMAT
Melilotus alba Desr.	MELALB
Monarda fistulosa L.	MONFIS
Monolepis nuttalliana (Schultes) Greene	MONNUT
Oenothera nuttallii Sweet	OENNUT
Orthocarpus luteus Nutt.	ORTLUT
Oxytropis deflexa (Pall.) DC.	OXYDEF
Oxytropis monticola A. Gray	OXYMON
Penstemon gracilis Nutt.	PENGRA
Penstemon procerus Dougl. *ex* Grah.	PENPRO
Petalostemon purpureum (Vent.) Rydb.	PETPUR
Phlox hoodii Richards.	PHLHOO
Plantago eriopoda Torr.	PLAERI
Plantago major L.	PLAMAJ
Polygonum arenastrum Jord. *ex* Bor.	POLARE
Polygonum convolvulus L.	POLCON
Polygonum douglasii Greene	POLDOU
Potentila gracilis Dougl. ex Hook.	POTGRA
Potentilla anserina L.	POTANS
Potentilla arguta Pursh	POTARG
Potentilla concinna Richards.	POTCON
Potentilla hippiana Lehm.	POTHIP
Potentilla norvegica L.	POTNOR
Potentilla pensylvanica L.	POTPEN
Psoralea argophylla Pursh	PSOARG
Psoralea esculenta Pursh	PSOESC
Ranunculus cardiophyllus Hook	RANCAR
Ranunculus pedatifidus J.E.Smith	RANPED

Rumex acetosella L.	RUMACE
Rumex crispus L.	RUMCRI
Salsola kali L.	SALKAL
Senecio canus Hook.	SENCAN
Senecio streptanthifolius Greene	SENSTR
Shepherdia canadensis (L.) Nutt.	SHECAN
Silene drummondii Hook.	SILDRU
Sisyrinchium montanum Greene	SISMON
Solanum triflorum Nutt.	SOLTRI
Solidago canadensis L.	SOLCAN
Solidago missouriensis Nutt.	SOLMIS
Solidago nemoralis Ait.	SOLNEM
Solidago rigida L.	SOLRIG
Solidago spathulata DC.	SOLSPA
Sonchus arvensis L.	SONARV
Spheralcea coccinea St. Hil.	SPHCOC
Stachys palustris L.	STAPAL
Stellaria longifolia Muhl.	STELON
Stellaria longipes Goldie	STELOG
Taraxacum officinale Weber	TAROFF
Thalictrum venulosum Trel.	THAVEN
Thermopsis rhombifolia (Nutt.) Richards.	THERHO
Thlaspi arvense L.	THLARV
Tragopogon dubius Scop.	TRADUB
Trifolium hybridum L.	TRIHYB
Trifolium pratense L.	TRIPRA
Trifolium repens L.	TRIREP
Veronica peregrina L.	VERPER
Vicia americana Muhl.	VICAME
Viola adunca J.E.Smith	VIOADU
Viola pedatifida G. Don.	VIOPED
Zizia aptera (A. Gray) Fern.	ZIZAPT

Shrubs and Trees

Amelanchier alnifolia Nutt.	AMEALN
Arctostaphylos uva-ursi (L.) Spreng.	ARCUVA
Caragana arborescens Lam.	CARARB
Corylus cornuta Marsh.	CORCOR
Elaeagnus commutata Bernh. *ex* Rydb.	ELACOM
Juniperus horizontalis Moench	JUNHOR
Populus tremuloides Michx.	POPTRE
Prunus virginiana L.	PRUVIR
Ribes oxyacanthoides L.	RIBOXY
Rosa spp.	ROSSPP
Rubus ideus L.	RUBIDE
Salix bebbiana Sarg.	SALBEB
Salix petiolaris J.E. Smith	SALPET
Symphoricarpos occidentalis Hook.	SYMOCC
Spirea alba Du Roi	SPIALB
Vaccinium myrtilloides Dougl. *ex* Hook.	VACMYR
Vaccinium vitis-idaea L.	VACVIT

Ferns and Fern Allies

Botrychium multifidum (Gmel.) Rupr.	BOTMUL
Selaginella densa Rydb.	SELDEN

Mosses

Abietinella abietina (Hedw.) Fleisch.	ABIABI
Amblystegium spp.	AMBSPP
Barbula spp.	BARSPP
Brachythecium salebrosum (Web. & Mohr)	BRASAL
Brachythecium spp.	BRASPP
Bryum argenteum Hedw.	BRYARG
Bryum caespiticium Hedw.	BRYCAE
Bryum spp.	BRYSPP
Campylium spp.	CAMSPP
Ceratodon purpureus (Hedw.) Brid.	CERPUR
Drepanocladus uncinatus (Hedw.) Warnst.	DREUNC
Eurhynchium pulchellum (Hedw.) Jenn.	EURPUL
Haplocladium spp.	HAPSPP
Hylocomium splendens (Hedw.) B.S.G.	HYLSPL
Pleurozium schreberi (Brid.) Mitt.	PLESCH
Polytrichum juniperinum Hedw.	POLJUN
Tortula ruralis (Hedw.) Gaertn., Meyer, & Scherb.	TORRUR

Lichens

Caloplaca spp.	CALSPP
Cetraria aculeata (Schreber) Fr.	CATACU
Cetraria ericetorum Opiz	CATERI
Cladina mitis (Sandst.) Hustich	CLAMIT
Cladonia cariosa (Ach.) Spreng.	CLACAR
Cladonia cenotea (Ach.) Spreng.	CLACEN
Cladonia chlorophaea (Somm.) Spreng.	CLACHL
Cladonia coniocraea (Florke) Springel	CLACON
Cladonia cornuta (L.) Hoffm.	CLACOR
Cladonia fimbriata (L.) Fr.	CLAFIM
Cladonia gracilis ssp. *turbinata* (Ach.) Ahti	CLAGRA
Cladonia macrophylla (Schaerer) Stenh.	CLAMAC
Cladonia multiformis Merr.	CLAMUL
Cladonia phyllophora Hoffm.	CLAPHY
Cladonia pocillum (Ach.) O. Rich.	CLAPOC
Cladonia pyxidata (L.) Hoffm.	CLAPYX
Cladonia scabriuscula (Del.) Leight.	CLASCA
Cladonia squamosa (Scop.) Hoffm.	CLASQU
Evernia mesomorpha Nyl.	EVEMES
Parmelia sulcata Tayl.	PARSUL
Peltigera didactyla (With.) Laundon	PELDID
Peltigera lepidophora (Vainio) Bitter	PELLEP
Peltigera rufescens (Weiss) Humb.	PELRUF
Physcia adscendens (Fr.) Oliv.	PHYADS
Physconia muscigena (Ach.) Poelt	PHYMUS
Usnea lapponica Vainio	USNLAP
Xanthoparmelia chlorochroa (Tuck.) Hale	XANCHL